A STUDY OF NORTHERN ATLANTIC COD (Gadus morhua) OF EASTERN NEWFOUNDLAND AND LABRADOR AS A METAPOPULATION

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by

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Abstract

I present a model of intrapopulation structure in northern Atlantic cod (*Gadus morhua*) inhabiting the coastal and continental shelf regions off northeast Newfoundland and Labrador based on metapopulation dynamics. I suggest that the metapopulation concept may best explain the historical patterns and present day observations of northern cod distribution. Evidence for subpopulation structure is assembled from new and published data sources, including studies of spawning time and location, migration behaviour, and genetic variation. A theoretical model of northern cod metapopulation dynamics is derived from the simple model of Levins (1970). I consider the various spawning components of northern cod historically centered on the offshore banks and in coastal bays as subpopulations of a northern cod metapopulation. I modify the Levins (1970) model by separating the probability of subpopulation extinction into two component probabilities representing: (1) natural processes and (2) the effects of fishing. Metapopulation theory predicts that fewer suitable areas (spawning grounds) will be occupied as population abundance declines. The corollary prediction is that as population abundance recovers, spawners will recolonize the currently unoccupied spawning areas. The agents of colonization may be migratory adult fish and straying larvae. The model supports the current view that overfishing may have played an important role in the extinction of northern subpopulations off Labrador.

Acknowledgements

First and foremost I would like to thank my supervisor, Dr. Joe Wroblewski, who, during the course of my research and in a timely manner gave me both the latitude of a peer and the guidance of an advisor. From Dr. Wroblewski I have come to learn the value of, when necessary, looking beyond the accepted paradigm for an explanation of the unexpected. I would also like to acknowledge the other members of my supervisory committee, Dr. David Schneider, Dr. George Rose, and Dr. John Brattey. The assistance of Dr. Schneider the during the 1995 field season was especially valuable. I appreciate the encouragement of Dr. Peter Shelton in applying a new idea to northern cod dynamics. Further thanks go to W. H. Hiscock, I. R. Bradbury, K. Morgan, L. Meade, and particularly to W. L. Bailey, for assistance in data collection in the field. Support for this research was provided by a number of sources, including the Centre For Fisheries Innovation, the Newfoundland and Labrador Department of Fisheries and Aquaculture, and the Department of Fisheries and Oceans. Personal support included the A. G. Hatcher Scholarship and Graduate Studies Fellowship from Memorial University of Newfoundland, together with grants awarded to Dr. Wroblewski.

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Chapter 1: Introduction

1.1 The northern cod stock complex

The northern cod stock (*Gadus morhua*) inhabits both the coastal and shelf regions of Labrador and northeast Newfoundland within the North Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K, and 3L (Figure 1.1). Northern cod is considered the southern component of the larger Labrador-East Newfoundland stock complex of Atlantic cod, extending from northern Labrador to the northern Grand Bank (Figure 1.1) (Templeman 1979; Lear and Parsons 1993). This stock complex is the most broadly distributed in the northwest Atlantic with a geographic range exceeding 15 degrees of latitude. For management purposes this stock complex was divided into two sections because the northern portion failed to recover following the collapse in abundance in the late 1960s due to overexploitation (Pinhorn 1976). These two portions are the Northern Labrador Portion located in NAFO Divisions 2G and 2H, and the Southern Labrador-East Newfoundland Portion ("northern cod") of NAFO Divisions 2J3KL (Lear and Parsons 1993).

The northern cod *population*, therefore, may be defined as those cod that live within the overall range of the complete Labrador-East Newfoundland stock complex of Atlantic cod as identified by Templeman (1979). For the purposes of this thesis, I consider the northern cod population to consist of those cod that occupy the range from Cape Chidley, at the northern tip of Labrador, to the northern portion of the Grand Bank

in NAFO Division 3L, and encompassing all of the coastal, shelf, and slope regions between these two areas (Figure 1.1). Hereinafter, the term "northern cod" will refer to the northern cod population in 2G, 2H, 2J, 3K, and 3L unless otherwise specified.

In general, northern cod inhabit both the coastal and shelf regions of Labrador and northeast Newfoundland, and undergo an annual offshore overwintering and spawning, inshore feeding migration (Lear 1984; reviewed in Lear and Green 1984). Spawning begins in late winter and may continue for up to four months for the overall population, with spawning occurring earlier in the north and progressively later to the south (Myers et al. 1993). The bulk of spawning occurs over the offshore banks (Templeman 1979; Taggart et al. 1994; Wroblewski et al. 1995), but some spawning might occur across the entire shelf (Hutchings et al. 1993). Spawning is also known to occur in the bays of northeast Newfoundland (Hutchings et al. 1993; Brattey 1997; Smedbol and Wroblewski 1997; Smedbol et al. 1998). After spawning offshore on the continental shelf, a substantial portion of the adults migrate to the inshore feeding areas for the summer, and return to the offshore in the late autumn and early winter (Lear 1984; Lear and Green 1984). The rest of the adults remain on the shelf (Taggart 1997).

The question of whether northern cod is a panmictic population is of considerable importance. Early studies indicated that northern cod may not be a panmictic unit, but rather may have contained a number of partially isolated subcomponents. Based on mark-recapture studies, Templeman (1962; 1979) postulated that northern cod contained many local populations,

> "each with its own tendency to return to home waters in the summer feeding season and with its own pattern of winter-spring distribution, but with much overlapping with adjacent local populations" (Templeman 1979).

Lear (1984) presented evidence for homing to specific offshore overwintering and spawning areas during the annual inshore-offshore migration, with some straying. These tagging studies also provide evidence for year round residency in particular offshore regions. Lear (1984) reported that some portion of the cod assemblage found on the northern Grand Bank does not migrate inshore following spawning, and resides on the Bank during the summer months.

Spawning and year-round residency are also characteristic of the coastal areas within the range of northern cod (see Chapters 2 and 3). A number of studies have provided evidence for spawning by cod along the northeast coast of Newfoundland (e.g. Brattey 1997; Smedbol and Wroblewski 1997; Smedbol et al. 1998). Mark-recapture data suggest a high degree of local residency within the coastal bays (Taggart et al. 1995; Wroblewski et al. 1996). Some fish occupy the inshore region throughout the year (Goddard et al. 1994; Wroblewski et al. 1994).

Analyses of microsatellite DNA allele frequency variation at the population level have provided evidence against the existence of a panmictic northern cod population. Recently Bentzen et al. (1996) detected small genetic differences between pooled samples of northern cod from the northwestern and southeastern areas of the northeast Newfoundland Shelf. These genetic studies have been extended to include samples from

inshore areas (see Chapters 2 and 3), resulting in the detection of five or more potential subcomponents of the northern cod population, located in both inshore and offshore areas (Ruzzante et al. 1996; Ruzzante et al. 1997; Ruzzante et al. 1998; Ruzzante et al. in press). A second, independent study also suggested the existence of several subcomponents in northern cod, using different microsatellite loci (T. Beacham, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC, personal communication).

1.2 The metapopulation model

A metapopulation is a set of local populations or subpopulations within some larger area (usually the population's range) where typically migration from one subpopulation to at least some other subpopulation is possible (Hanskii and Simberloff 1997). Metapopulation theory describes the spatial dynamics of interconnected subpopulations. The metapopulation's overall range is expressed as the total of discrete areas of suitable and unsuitable habitat. The degree of segregation between subpopulations may range from slight to almost complete isolation, depending upon factors such as the distance between areas of suitable habitat, the magnitude of variation in habitat quality, life history characteristics (e.g. discrete life stages), and the dispersive abilities of the species (e.g. Harrison and Taylor 1997). Exchange between the subpopulations of the metapopulation prevents the development of separate, autonomous populations. As a result, subpopulations in a metapopulation may not (and need not) be

genetically distinct, although such differentiation is suggestive of the existence of metapopulation structure with very low levels of exchange between subpopulations.

In the simplest metapopulation model first proposed by Levins (1970), there are three assumptions: habitat areas have the same geographic extent and degree of isolation, each subpopulation has separate local population dynamics, and the rate of exchange (migration) of individuals among subpopulations is too low to affect local population dynamics. Local dynamics occur on a faster time scale than metapopulation dynamics. Hanskii and Simberloff (1997) suggest that of major importance is the idea of discrete local breeding populations connected by migration.

In the Levins model, habitats are considered either occupied or unoccupied. During each time step of the model (usually annual, such as breeding season to breeding season), each habitat area has a probability of being occupied or empty. The Levins (1970) model, in its simplest form, can be expressed as:

1.1) $$\frac{dP}{dt} = mP(1 - P) - eP$$

where P is the fraction of habitat patches occupied at time t, m is the "colonization" parameter, and e is the "extinction" parameter. The rate of colonization of empty habitats is assumed to be proportional to P, the fraction of occupied habitats, and to $(1 - P)$, the fraction of unoccupied habitats.

The equilibrium value of P is:

1.2) $$\hat{P} = 1 - \frac{e}{m}$$

and therefore the metapopulation will persist as long as $e/m < 1$. In other words, for persistence to occur, recolonization must occur at a sufficiently high rate within the metapopulation to offset the rate of extinctions (Hanskii 1997). Persistence may be augmented by migration (exchange) among patches (Hanskii 1991), and with increasing number of suitable areas and local subpopulations (Harrison and Taylor 1997).

Although abundance is not explicitly included in the model, investigations by Hanskii (1991) have shown that m is also proportional to overall metapopulation abundance, due to a "rescue effect" at higher abundances in which immigrants from other subpopulations enhance subpopulation persistence. The model, therefore, can be viewed as calculating the "occupancy" of suitable habitats within a population's range. Extinction is considered to be equally likely for all habitats (a constant), resulting in a subpopulation lifetime of order $1/e$. The abundances of local subpopulations (within each habitat) are assumed to be either 0 (empty) or at the carrying capacity (full). Therefore, areas of suitable habitat are considered either empty or full.

Models of metapopulation structure of various forms have been used to describe the spatial dynamics of many terrestrial and aquatic species. Some examples include shrews (Peltonen and Hanskii 1991), butterflies (Hanskii 1994a), malleefowl (Day and Possingham 1995), and river fishes (Gotelli and Kelley 1993). These examples from diverse taxa hold in common the occupation of ranges comprised of heterogenous habitat.

1.3 Northern cod as a metapopulation

I contend that during the spawning period northern Atlantic cod (*Gadus morhua*) may be viewed as a metapopulation, and therefore metapopulation models may best explain the structure in spatial distribution observed in mark-recapture and genetic studies of northern Atlantic cod. The model that I propose uses a strict definition of "habitat". Suitable habitats are defined as the overwintering/spawning areas, of both inshore and offshore subpopulations of the northern cod population. These local populations are identified using a number of criteria: genetic distinctiveness (microsatellite DNA allele frequency variation), morphometrics (length-at-age, weight-at-age, fecundity-at-age), and residency in or interannual fidelity to discrete spawning areas. How such structure may form is unclear. The physical and (or) behavioural processes that result in the semi-isolation of these subpopulations in an open oceanic system are poorly known. For instance, it is not understood how juveniles might return to their natal grounds. However, the evidence points to the existence of such structure, regardless of whether or not the subpopulations are genetically discrete.

The genetic data (e.g. Ruzzante et al. 1997; Ruzzante et al. in press; see Chapter 3) suggest that some subpopulations are more isolated reproductively than others. This departs from the simplest metapopulation model of Levins (1970) (see Figure 1.2a), but metapopulations that conform to the assumptions of Levins (1970) may be rare (Harrison and Taylor 1997). Northern cod may conform to the "mixed structure" metapopulation model of Harrison and Taylor (1997; Figure 1e, page 28), wherein the metapopulation

includes patches combined by relatively high rates of exchange, together with more isolated peripheral ones (Figure 1.2b).

The application of the metapopulation concept to northern cod is provided in Figures 1.2c and 1.3. For genetic differentiation to develop and be maintained among subpopulations in the absence of selection, some process of local larval retention or natal philopatry is necessary. Figure 1.2c presents some possible mechanisms that may result in this semi-isolation of subpopulations. Prevailing winds are westerly or southwesterly during the spring and summer spawning season (spawning begins earlier in March to the north), but wind direction does vary. Events such as storms can have a substantial effect on the direction of drift from year to year (see Helbig et al. 1992). Larvae that settle away from nursery grounds may be lost to the subpopulation (e.g. Sinclair 1988), but may also function in colonization of new habitat. As juvenile members of offshore subpopulations grow, they eventually join the adult spawning-feeding migration (Harden-Jones 1968; Lear and Green 1984). Conversely, the eggs and larvae of inshore subpopulations may be retained within the bay, and most juveniles and adults may reside within the inshore zone year-round.

I model northern cod spatial distributions only during the spawning period. As a consequence I do not consider the same spatial structure as have other studies of dynamic population range in Atlantic cod, which have concentrated on spatial distribution during the post-spawning, feeding season (Swain and Wade 1993; Marshall and Frank 1994; Marshall and Frank 1995). Rather, the focus of this study is on the relative temporal stability of geographically discrete spawning components, as they might relate to

metapopulation structure, genetic architecture, and rate of exchange between spawning groups.

1.4 Subpopulations of the northern cod metapopulation

First I consider the various spawning components of northern cod historically centred on the offshore banks and in coastal bays as subpopulations of a metapopulation ranging over 190,000 km^2 of continental shelf. Evidence for the past and present existence for these major spawning locations is derived from a variety of data sources. These subpopulations (spawning components) have been delineated in Figure 1.3. While some spawning may occur throughout the continental shelf (Hutchings et al. 1993), by far the bulk of spawning by the northern cod stock is concentrated in the areas noted in Figure 1.3.

The most northerly area identified as a major spawning location is the shelf break area of Saglek Bank (Figure 1.3) in NAFO Division 2G (Figure 1.1). Postolaky (1965) sampled prespawning and spawning aggregations in this area during the spring (March-April), at depths of 280-350 m. Newly spawned cod eggs were also sampled in this area during April (Postolaky 1965). The Saglek Bank area produced the highest number of recently spawned eggs in his study. The next major spawning location was determined to lie along the shelf break of Nain Bank (Figure 1.3), in NAFO Division 2H (Figure 1.1). Postolaky (1965) captured spawning cod and cod eggs in this area in April. The area of Makkovik and Harrison Banks (Figure 1.3) near the Division 2H-2J border (Figure 1.1) is

included in the metapopulation model because of the discovery of early stage cod eggs in this region by Serebryakov (1967), again in the early spring.

Major spawning areas can be found along the eastern slopes of Hamilton Bank, Belle Isle Bank, and Funk Island Bank (Figure 1.3). Early evidence from the 1960s of cod egg (Serebryakov 1967) and spawning aggregations (Templeman and May 1965) has been reported for the slope regions of the banks. Wroblewski et al. (1995), using data from thousands of trawl sets by commercial trawlers, found that many cod spawned along the shelf edge. More recently, Hutchings (1996) reported interannually consistent, high density catches of cod in research trawl survey tows associated with these banks during the late fall from 1981-1992. In light of the overall evidence, the three banks and adjacent areas have been designated as two spawning areas in this study (Hamilton Bank and Belle Isle-Funk Isle Banks).

Another spawning area has been identified along the eastern continental shelf and slope in the north of Division 3L (Figures 1.1 and 1.3), at the eastern terminus of the inshore migration path along the Bonavista Corridor (Rose 1993). Hutchings (1996) documented high density catches from research trawl survey tows in this area during October through December, from 1981-1992. In more recent years, cod spawning in this area has been documented on the eastern shelf (Rose et al. 1995) and slope (Wroblewski et al. 1995). Research trawl surveys have captured cod in spawning condition in this spawning zone (Hutchings et al. 1993).

The most southerly spawning region for northern cod is located on the northern section of the Grand Banks (Figure 1.3) in Division 3L (Figure 1.1). Evidence for cod

spawning in this area has been reported by several sources: research trawl surveys (Hutchings et al. 1993), tagging studies (Templeman 1962; Templeman and Fleming 1962), and commercial catches (Kulka et al. 1995; Wroblewski et al. 1995).

Spawning areas have been identified in the coastal areas of the population range of northern cod. Cod in spawning condition have been caught, and eggs and larvae have been sampled at several locations in Gilbert Bay (J. Wroblewski and J. Green, Memorial University, St. John's, unpublished data), however few data exist on possible inshore spawning locations along coastal Labrador. As a result of the paucity of data in the coastal Labrador region, only the Gilbert Bay area is identified as a known spawning area (Figure 1.3).

There are historical reports of an inshore fishery for northern cod in Groswater Bay, and Sandwich Bay, Labrador (Figure 1.3) (H. Best, Labrador Institute, Memorial University of Newfoundland, St. John's, personal communication). This fishery ceased in the 1960s after heavy fishing by foreign trawlers along the Labrador coast. The extinction of a slow growing coastal subpopulation may be the cause of the collapse of the fishery in Groswater and Sandwich Bays. This location is noted in Figure 1.3, but is not given the status of subpopulation due to the lack of data.

Much more data exists for inshore spawning along the Northeast coast of Newfoundland. Evidence for spawning in the coastal bays is provided by egg and larval surveys (Smedbol and Wroblewski 1997; Smedbol et al. 1998), the presence of pelagic (Anderson and Dalley 1997) and post-settlement (Methven and Badjic 1994; Pinsent and Methven 1997) juveniles, research trawl and gillnet surveys (Hutchings et al. 1993),

analysis of gonadal condition of commercial catches (Smedbol and Wroblewski 1997), sampling of individuals from spawning aggregations (Brattey 1997; Smedbol and Wroblewski 1997), and from interviews with local fishers (Neis et al. submitted). Most of these data were obtained from Trinity Bay (Figure 1.3). While there is some evidence for residency in adjacent Bonavista and Conception Bays, I did not formally include these bays in the analysis as spawning areas as definitive studies of spawning have yet to be undertaken.

At high population abundance, metapopulation models incorporating even a relatively low degree of exchange predict the occupancy of a high proportion of suitable habitats (e.g. Hanski 1991). In the metapopulation model for northern cod, this translates to the occupancy of most, if not all, of the major spawning areas in years of high population abundance. Tagging studies reveal that a small proportion of cod stray long distances from year to year, and also point to the limited exchange of adults between all major spawning components (Lear 1984; Taggart et al. 1994). This exchange is allowed in a metapopulation model. I propose that during the period of high abundance in the 1960s (Bishop et al. 1993), all these subpopulations of northern cod existed. Several authors have noted this spatial "stability" in spawning locations, as evidenced from mark-recapture studies (Templeman 1979; Lear 1984; Taggart et al. 1994), and to a lesser extent from research trawling surveys (Hutchings 1996) and data derived from commercial trawlers (Wroblewski et al. 1995).

When the northern cod population collapsed in the early 1990s mainly due to overfishing (Hutchings and Myers 1994), the spatial coverage of the population apparently

did not simply contract from the outer limits of its range. Rather, the fish were found overwintering/spawning at fewer areas (Kulka et al. 1995; Hutchings 1996; Rice 1997). The change in distribution has been interpreted as a shift in occupancy from the north to the south of the range due to environmental changes (deYoung and Rose 1993) and (or) shifts in prey distribution (Rose et al. 1994). Alternatively, overfishing and (or) unfavourable environmental conditions may have forced some subpopulations to commercial extinction (Larkin 1977; Myers et al. 1997a). The current spatial structure of the population during the overwintering/spawning season appears to be sharply discrete, with aggregations of overwintering/spawning adults now much smaller in size and occupying fewer areas, including Smith Sound, Trinity Bay (Smedbol et al. 1998) and Tobins Point (49° 30' N, 50° 30' W) on the northern Grand Bank (Rose 1996). In recent years, only small numbers of cod are found dispersed across the continental shelf between these areas (Hutchings 1996; Shelton et al. 1996; Rice 1997).

1.5 Objectives of this research

In this dissertation I present published and unpublished evidence for the existence of subpopulations of northern cod in two inshore areas, Trinity Bay (Chapter 2) and Gilbert Bay, southeastern Labrador (Chapter 3). Accepting that northern cod may be viewed as a metapopulation (Figure 1.3), I then use the simplest form of the metapopulation model (Levins 1970) to: (*i*) model relationships among subpopulations of northern cod, (*ii*) estimate values for the colonization and extinction parameters for the model, and (*iii*) include the effect of fishing in the model. Finally, I discuss the

implications for recolonization from currently occupied areas (inshore) to unoccupied areas (offshore).

My dissertation, therefore, has two major objectives. The first objective is to establish that inshore subpopulations of northern cod exist. The study of Trinity Bay is presented in Chapter 2. The analysis of Gilbert Bay is presented in Chapter 3. The second objective is to construct a metapopulation model for northern cod. The modelling study is presented in Chapter 4. In this modelling endeavour, the first task is to derive approximate parameter values. Following development of the basic model, I consider the possible effect of commercial harvest on the spatial dynamics of northern cod, and incorporate a fishing effect into the model. I then use the model to develop predictions of how the spatial dynamics of the metapopulation might behave during periods of decline in population abundance. Finally, I develop predictions for the rate of spatial recolonization of unoccupied spawning areas during a period of future recovery.

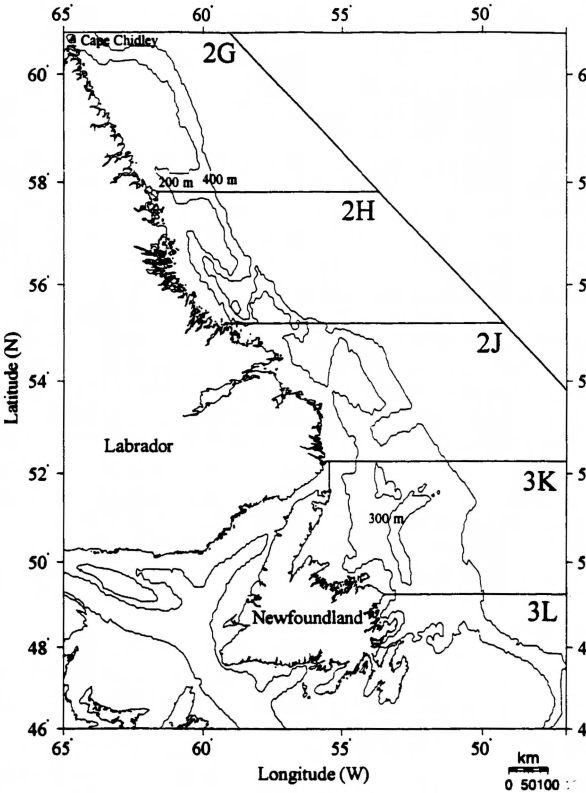

Figure 1.1. North Atlantic Fisheries Organization Divisions in the study area.

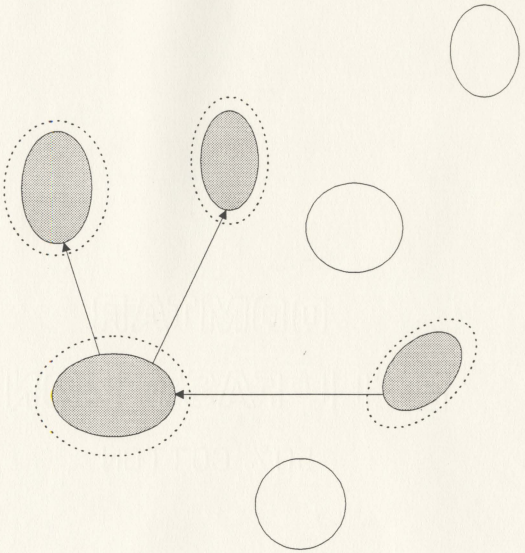

Figure 1.2a. Classic Levins (1970) metapopulation, modified from Figure 1a of Harrison and Taylor (1997). Filled circles, occupied habitat patches; empty circles, vacant habitat patches; dotted lines, boundaries of local populations; arrows, dispersal.

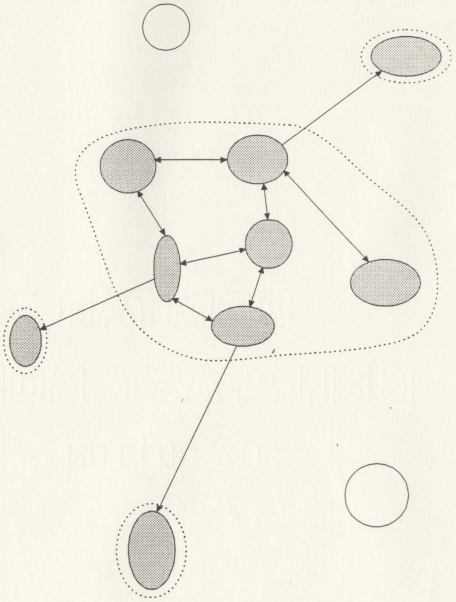

Figure 1.2b. Mixed structure metapopulation, modified from Figure 1e of Harrison and Taylor (1997). This metapopulation exhibits a structure that includes clustered and isolated patches. Some patches are combined by relatively high rates of exchange into a single subpopulation. Symbols as in Figure 1.2a.

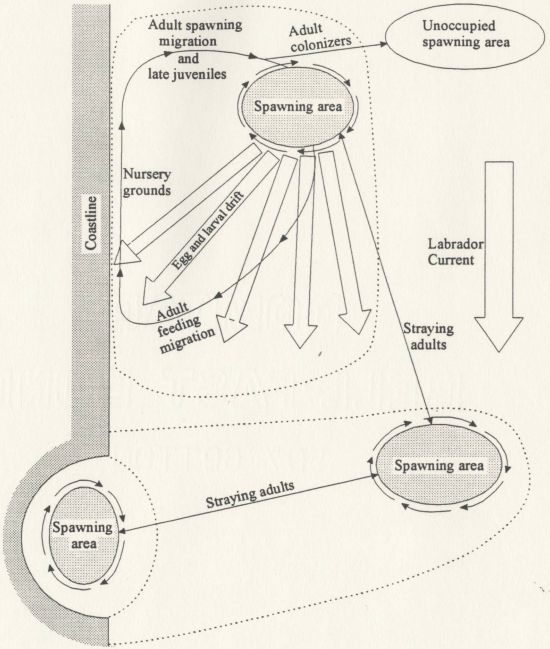

Figure 1.2c. Northern cod as a metapopulation. Dotted lines are boundaries of subpopulations; arrows encircling spawning areas denote possible retention mechanisms. Overlayed on the structure of one subpopulation are the distributions of the egg/larval, juvenile, and adult life history stages.

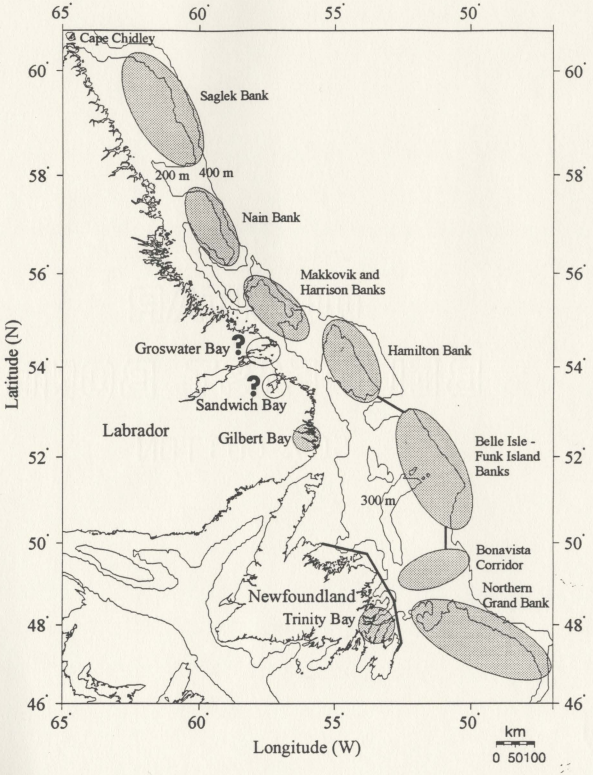

Figure 1.3. Proposed subpopulations of northern cod. See text for details. Solid lines link areas that may contain a single subpopulation.

Chapter 2: A subpopulation in Trinity Bay

2.1 Introduction

Before constructing a metapopulation model of northern cod, I will first review all of the evidence for spatially structured subpopulations within the overall geographic range of northern cod. While there was compelling historical evidence for the existence of offshore stocks associated with the major offshore banks (see Chapter 1), the evidence for putative local populations in the inshore areas is more recent. Below I discuss evidence for the existence of a local population of cod in Trinity Bay drawn from data concerning (*i*) spawning times and locations, (*ii*) mark-recapture analysis of adult cod, and (*iii*) spatial variance of microsatellite DNA allele frequencies in northern cod.

2.2 Spawning

Reports of cod in spawning condition in major bays off northeast Newfoundland (Figure 2.1) are not new (Neilson 1894; Neilson 1895; Graham 1922). Hutchings et al. (1993) presented data from research gillnet surveys on the presence of cod in spawning condition in Trinity Bay during the spring in the years 1967-68. Lawson and Rose (1999) have documented cod spawning in Placentia Bay on the south coast of Newfoundland.

Inshore spawning has been observed in cod populations found in other regions of the North Atlantic. McKenzie (1940) provided documentation of autumn spawning in Halifax Harbour, Nova Scotia. Cod spawn annually in the fjords of Norway (Trout 1957;

Gødø and Sunnanå 1984; Jakobsen 1987). Apparently inshore spawning is part of the reproductive biology of Atlantic cod. Therefore, spawning would be expected to occur in Newfoundland inshore waters as well.

Smedbol and Wroblewski (1997) determined that Atlantic cod spawned in Trinity Bay (Figure 2.1) in the early summer during each year of the period from 1991 to 1993. This conclusion was based on (*i*) the observed progressive maturation of bay cod from spawning to spent condition, (*ii*) direct observation of a spawning aggregation of cod over Heart's Ease Ledge, and (*iii*) the presence of recently spawned ($\leq$ 10 days) cod eggs in the study region (Figure 2.2).

The data from commercial catches in the Random Island area of Trinity Bay document the development of gonadal tissue in adult cod in the bay during the spring of three consecutive years (1991-1993). A peak in the proportion of adults with gonads in spawning condition or partly spent from mid-June through mid-July led the authors to suggest the bulk of spawning occurred during this late spring and early summer interval in those years.

Direct acoustic observations (Smedbol and Wroblewski 1997) in late June-early July led to the detection of a spawning aggregation over Heart's Ease Ledge (Figure 2.2). This spawning occurred within the temporal range for inshore spawning estimated by Smedbol and Wroblewski (1997) from the commercial catch data in the region in 1991 and 1992.

The third piece of evidence was obtained from ichthyoplankton surveys in the spring and summer of 1991 and 1993 (Smedbol and Wroblewski 1997), and the summer

of 1995. Descriptions of the sampling protocol and statistical analyses are provided by Smedbol et al. (1998). Sampling stations are presented in Figure 2.2.

Estimated ages of cod eggs collected in the region during each year of the study provide spawning times that are also within the peak spawning period (late June-early July) delineated by the commercial catch data (Smedbol and Wroblewski 1997, Smedbol et al. 1998). In 1995 a relatively large aggregation (16 800 tonnes Rose 1996) was discovered in Smith Sound, Trinity Bay (Figure 2.2). The reproductive output of this aggregation was monitored and evaluated relative to egg densities in 1991 and 1993 (Table 2.1, 2.2). The spawning of this aggregation resulted in elevated concentrations of eggs relative to 1991 and 1993 (Table 2.2, Figure 2.3). However, this did not result in a detectable increase in the number of settled age 0 juveniles in the region (Smedbol et al. 1998).

The spawning period estimated in the study by Smedbol and Wroblewski (1997) is consistent with other research findings. Brattey (1997) reported similar spawning times for cod in the area during 1996. Methven and Bajdik (1994) reported that the timing of the initial appearance and settlement of pelagic juvenile cod in coastal regions of Trinity Bay is usually during the last two weeks of August and the first two weeks of September. These authors reported two periods of high abundance of pelagically coloured juvenile cod (August-September and October-November) at the southern end of Trinity Bay for the years 1982-1983 and 1989-1990. Calculated estimates of the time of fertilization of the September-October juveniles coincide with the June-early July peak spawning interval estimated by Smedbol and Wroblewski (1997).

A study by Pinsent and Methven (1997) provides further evidence that Trinity Bay is a spawning location of cod. The authors used daily growth increments of the lapillus otolith to backcalculate the date of spawning of individual age 0 cod. Pinsent and Methven (1997) conclude that age 0 cod caught in August (with a late May hatch date) were probably spawned in Trinity Bay because of the difference between spawning times within Trinity Bay (Smedbol and Wroblewski 1997) and in offshore areas (Myers et al. 1993).

Anderson et al. (1995) back-calculated spawning times from lengths of larval cod found in Trinity Bay. They computed peaks in cod spawning of May, 1984 (day 130-140), and late May/early June, 1985 (day 140-160). The authors concluded that an offshore source for these larvae was unlikely, and that these larvae probably originated from inshore spawning in the Trinity Bay area. In contrast, Anderson et al. (1995) computed an April peak in offshore spawning for the same years.

There is historical data indicating that spawning is persistent over time, and not simply a recent occurrence. Graham (1922) and Thompson (1943) reported the presence of cod in spawning condition in Trinity Bay during the summer months (day 121-181). Examining historical data, Hutchings et al. (1993) reported the presence of adult cod in spawning condition in May/June, 1967 (day 121-181) at four locations in Trinity Bay.

2.3 Behaviour

2.3.1 Overwintering and residency of cod in Trinity Bay

Studies involving the sonic tagging and tracking of adult cod have demonstrated that adult cod overwinter in the Random Island area of Trinity Bay (Figure 2.2) (Goddard et al. 1994; Wroblewski et al. 1994; Wroblewski et al. 1996). In these studies, many (14 of 26 total) of the fish released with acoustic transmitters around Random Island in the late autumn were relocated in the area during the following spring. Some fish tagged in these and related studies were caught by fishers in subsequent years inside the Random Island study area (Wroblewski et al. 1996; Hiscock, 1997; J. Wroblewski and W. Hiscock, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF unpublished data).

Strong evidence for residency within Trinity Bay by adult northern cod (winter and summer) has been provided by investigations using mark-recapture data. Wroblewski et al. (1996) analysed tagging data from the Random Island region compiled by Taggart et al. (1995). During the winter and early spring of 1988, 1990, and 1991 a total of 5021 cod were tagged and released in Southwest Arm, Trinity Bay (Figure 2.2). By January 1, 1995, a total of 1398 of these fish had been recaptured, with the month and location of capture reported. By the end of the first overwintering period 95 % of the recapture locations were within 30 nm of the release site; all but 1 recapture were within 60 nm. Through November of the first year of release, 83 % of recaptures were within 30 nm of the release site; all but 12 were within 60 nm. Following the end of the second overwintering period, a further 40 of 49 total recaptures occurred within 60 nm (including Bonavista Bay). If returns from the first year of release are ignored, 68% of returns came from within 30 nm of the release site, and 83 % from within 60 nm. This pattern

continued through the third and fourth years post-release, with reduced recaptures recorded.

In a reanalysis of the same mark-recapture data, Taggart et al. (1998), using objectively determined contours derived from the spatial pattern of the recapture data, reported that > 70 % of the recaptures occurred within 30 nm of the original tagging location, and < 20 % of returns were farther than 60 nm from the location of release. Returns during the first six months following release were excluded. Most fish were caught relatively close to their release site. This suggests that most individuals did not travel very far from their area of release, or later returned to the area in subsequent months. Recaptures in Bonavista Bay suggest that a portion of the fish in Trinity Bay may migrate between bays, as is also suggested by microsattelite DNA analysis (T. Beacham, Department of Fisheries and Oceans, Pacific Biological Station, Nanaimo, BC, personal communication). The relatively high probability of recapture near the release location is compatible with the hypothesis of a local, resident population of cod in Trinity Bay.

2.4 Genetics

Despite evidence from migration studies pointing to subpopulation structure (the residency of individuals in spawning areas) arising from tagging data, until recently studies of population genetics have been equivocal concerning the possible existence of genetically distinct subpopulations within the northern cod stock complex. Studies based on mitochondrial DNA variation have provided no evidence for population differentiation across the geographic range of northern cod (Carr and Marshall 1991a; Carr and Marshall

1991b; Pepin and Carr 1993). Comparisons in mDNA variation also did not resolve population segregation between cod from inshore and offshore regions (Carr et al. 1995).

Unlike mtDNA analyses, studies using microsatellite nuclear DNA have resolved genetic differences between cod in Trinity Bay and offshore components of the northern cod population. Ruzzante et al. (1996) used microsatellite DNA to resolve statistically significant levels of allele frequency variation among samples gathered in spring and early summer from the Random Island area of Trinity Bay and samples from offshore locations. The samples from Trinity Bay included fish from the Heart's Ease Ledge spawning aggregation reported in Smedbol and Wroblewski (1997). Subpopulation structure was detected only when inshore cod with high antifreeze glycoprotein levels, which are indicative of overwintering in subzero water (Goddard et al. 1994), were compared to offshore samples. The authors concluded that cod overwintering inshore were genetically distinct even though individuals from offshore and inshore areas mix inshore during the summer feeding migration.

Temporal stability of microsatellite markers is a key factor because if the marker frequencies change from year to year, there may be other processes at work and other factors involved in allele frequency. Genetic samples collected in subsequent years and analysed by Ruzzante et al. (1997) also showed the same genetic differentiation between offshore cod and cod from Trinity Bay. This led Ruzzante et al. (1997) to conclude that the genetic pattern reported by Ruzzante et al. (1996) was temporally stable.

2.5 Conclusion

I conclude that there is ample evidence supplied by studies examining the life history and population genetics of cod within Trinity Bay to support the hypothesis that a local subpopulation of the northern cod population exists in the bay. Local residency in a spawning area is supported by the year-round occupation of Trinity Bay by adults as evidenced by sonic tagging and tracking studies, together with traditional mark-recapture and ichthyoplankton investigations. The presence of a local subpopulation is further supported by genetic differentiation between cod in Trinity Bay and offshore areas when sampled during the prespawning and spawning periods. Such genetic differences can only occur under at least partial reproductive isolation among breeding units.

Table 2.1. Cod egg densities (eggs·m^{-3}) at each station and survey period. HEL 1, 2, and 3 represent repeated samples at the Heart's Ease Ledge station (after Smedbol et al. 1998).

Station	June 1991 (day 168)	July 1991 (day 198)	June-July 1993 (days 180-187)	June 1995 (days 171-173)
S1	---	---	---	1.448
S2	---	---	---	0.783
S3	---	---	---	0.387
S4	0.017	0.116	0.104	---
S5	0.006	---	0.096	---
S6	---	0.129	0.445	0.12
S7	0.008	0.01	0.085	1.119
S8	0.011	0.006	0.057	---
S9	0.007	0.004	0.036	0.517
S10	0.009	0.007	0.011	---
S11	0.025	0.002	0.002	0.115
S12	---	---	0.014	---
S13	0.116	0.022	---	---
HEL (1)	---	---	0.078	0.662
HEL (2)	---	---	0.088	---
HEL (3)	---	---	0.012	---
S14	---	---	---	0.37
S15	---	---	---	0.122
S16	---	---	---	0.227
S17	---	---	---	0.266
S18*	---	---	0.001	---
S19*	---	---	0.001	---
S20	---	---	---	0.524
S21*	---	---	0.001	---
S22*	---	---	0.038	---

Table 2.2. Comparison of egg densities (eggs·m^{-3}) in 1995 and pooled surveys in 1991 and 1993 in Trinity Bay. From Smedbol et al. (1998).

		Ratio of means, all stations		Mean density common stations only	Ratio of means, common stations only	
	Mean density	1995/sample year	1995/pooled years		1995/ sample year	1995/ pooled years
June 1991 Day 168	0.025	20.5	14	0.013	45	30
July 1991 Day 198	0.037	13.9		0.005	117	
J-J 1993 Day 180-187	0.064	7.97		0.041	14	
June 1995 Day 171-173	0.512			0.584		

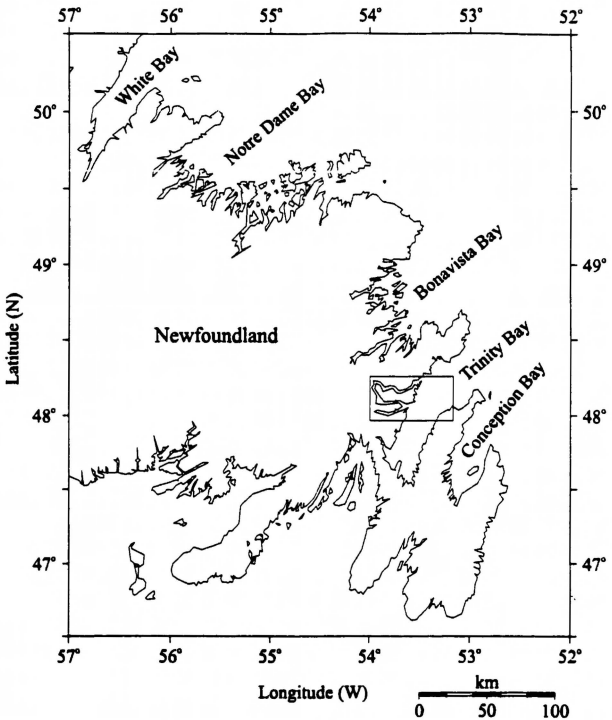

Figure 2.1. Map of the northeast coast of Newfoundland. The inset box in Trinity Bay provides the location of the ichthyoplankton survey area presented in Figure 2.2. Modified from Smedbol et al. (1998).

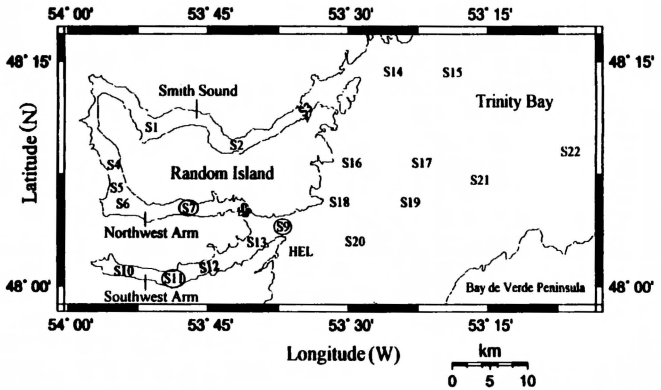

Figure 2.2. Map of the Random Island area of Trinity Bay showing the ichthyoplankton survey sites sampled in 1991, 1993, and 1995. HEL is Heart's Ease Ledge, a known spawning area (Smedbol and Wroblewski 1997). The three stations that were sampled during every survey period (S7, S9, and S11) are encircled; these are the "common stations" found in Table 2.2. From Smedbol et al. (1998).

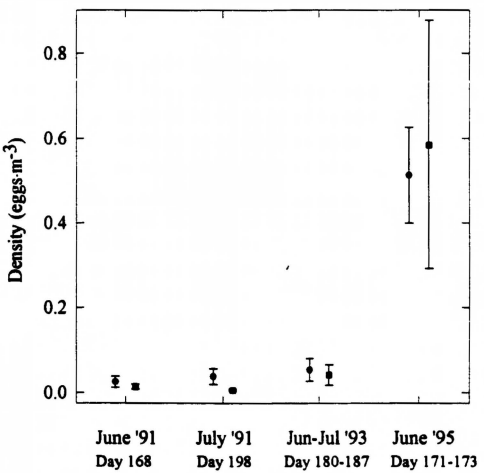

Figure 2.3. Mean cod egg density from stations in the Random Island area of Trinity Bay calculated from all stations (circles), and only stations S7, S9, and S11 (squares), which were sampled in every survey period (1991, 1993, and 1995). Error bars represent standard errors. From Smedbol et al. (1998).

Chapter 3: A subpopulation in Gilbert Bay

3.1 Introduction

The purpose of this investigation was to determine if the coastal regions of Labrador also supported inshore subpopulations of northern cod. The more northerly location greatly reduces the likelihood that if a local subpopulation exists, its internal dynamics would be associated with that of the Trinity Bay subpopulation, which lies approximately 4.5 degrees of latitude further south (Figure 3.1).

In addition to its more northerly location, Gilbert Bay (approximately 52° 35' N, 55° 55' W) differs in physical structure from Trinity Bay. Gilbert Bay is a nearly enclosed embayment due to its many islands and highly irregular shoreline (Figure 3.2), and does not contain drowned fjords such as Smith Sound, Northwest Arm, and Southwest Arm in Trinity Bay (Figure 2.2). Also, portions of Trinity Bay are greater than 300 m in depth, whereas all of Gilbert Bay is less than 100 m in depth. The historical fishery for northern cod in Gilbert Bay was small, localized, and much more recent (Powell 1987) relative to the historical inshore fishery of Trinity Bay, which has existed in some form for hundreds of years (Hutchings and Myers 1995).

I hypothesize that the geography (semi-enclosed embayment) of Gilbert Bay may lead to at least some degree of reproductive isolation of local cod, resulting in the formation of a discrete local subpopulation belonging to the northern cod metapopulation. The hypothesis of the existence of a subpopulation in Gilbert Bay was tested in two ways:

(*i*) the comparison of morphometric and life history traits of cod from Gilbert Bay to cod sampled in Trinity Bay (a known inshore local subpopulation) and to cod captured offshore at latitudes similar to that of Gilbert Bay, and (*ii*) comparison of microsatellite DNA allele frequency distributions of cod from Gilbert Bay to cod from other areas within the range of northern cod.

3.2 Materials and Methods

3.2.1 Sampling

Samples of adult cod were collected from six locations within Gilbert Bay during 1996-1997. All fish were captured with rod and lure. A total of n = 159 fish were sampled during the two years. In August 1996, a total of 122 cod were captured at two locations (52° 36.2' N, 55° 55' W, and 52° 35.88' N, 55° 58.63' W) (Figure 3.2), and in October n = 12 fish were collected from two separate locations (52° 34.25' N, 55° 59.65' W, and 52° 37.25' N, 56° 01.55' W) (Figure 3.2). The cod collected in October were released following measurement and blood sampling for genetic and antifreeze glycoprotein analysis (see procedure below). As a result of the lack of age determination (otoliths were not collected), these 12 fish from October 1996 were excluded from the morphometric analysis. During May 1997, a further 37 cod were obtained at two other nearby locations (52° 35.38' N, 55° 55.75' W, and 52° 34.93' N, 56° 01.25' W) (Figure 3.2).

Fish sampled in Trinity Bay, on April 24, 1995 were used as a comparison group in the following analyses. The fish were captured with an otter trawl (#36 Yankee) with

11.3 cm stretched mesh and a codend liner. The trawl was towed for five minutes at a depth of 154 m.

In samples from both Trinity Bay and Gilbert Bay, individual age, sex, mass, and length were recorded. In the August 1996 sample (n = 122) from Gilbert Bay, only a subsample (n = 24) was weighed. Otoliths were removed and used for age determination. Stage of sexual maturity was designated following the criteria of Templeman et al. (1978). Blood samples for genetic and antifreeze glycoprotein analyses were collected from each fish in the October 1996 and May 1997 samples from Gilbert Bay only.

3.2.2 Antifreeze glycoprotein analysis

Cod collected from Trinity Bay in April 1995 and from Gilbert Bay in May 1997 were examined for serum antifreeze activity (Ruzzante et al. in press). Following capture, blood samples were obtained from a caudal blood vessel using a 21 or 23 gauge needle and a 3 cm^3 syringe. Samples were immediately transferred to a Vacutainer (Becton Dickinson) containing sodium heparin. The samples were held on ice until they could be centrifuged later in the day. Following centrifugation the plasma samples were removed from the Vacutainers and placed in 1.5 ml Eppendorf tubes and stored at -20 °C. Samples were later analysed for antifreeze activity at Memorial University's Marine Science Research Laboratory (for methods see Goddard et al. 1992). The level of antifreeze activity is evaluated by measuring thermal hysteresis; the difference between the melting and freezing point of the sample. Thermal hysteresis is directly proportional to the concentration of antifreeze glycoprotein in the blood plasma (Kao et al. 1986). Goddard et al. (1994) has shown that in northern cod thermal hysteresis functions as a physiological

time tag to estimate the duration an individual fish has been resident in sub-zero temperature water.

3.2.3 Fecundity

Reproductive capacity, the amount of energy allocated to reproduction, and the resultant population growth rate are interdependent life history traits that can be used to differentiate between conspecific populations. These traits may be phenotypically plastic, and differ among subpopulations due to variation in the local environment (e.g. temperature, prey abundance). Potential fecundity, defined as the number of vitellogenic oocytes in an ovary prior to spawning (Kjesbu et al. 1991), can be used as a proxy metric of reproductive effort for a particular spawning season. Potential fecundity-at-age, similar to length- and weight-at-age, may vary in cod as a result of differing environmental regimes (and perhaps genotype) between sampling locations (May 1967).

The potential fecundities of a subsample (n = 15) of the adult female cod captured in Gilbert Bay in May 1997 were estimated by Ruzzante et al. (in press) using the gravimetric wet weight method (Bagenal 1978; Kjesbu 1989). Three subsamples of ovarian tissue (each 100-200 mg) were taken from the middle of the right ovary. Vitellogenic oocytes > 250 μm in each subsample were counted using a dissecting microscope with an ocular micrometer. Subsample counts were averaged. Potential fecundity of each female then was calculated using the wet weight of the ovary. Relative fecundity was calculated following Kjesbu and Holm (1994) such that:

3.1) $$Relative\ fecundity = \frac{potential\ fecundity\ (oocytes)}{somatic\ weight\ (g)}$$

These fecundities were compared to published fecundity estimates for offshore Labrador (NAFO Div. 2J; May 1967) and Trinity Bay (Pinhorn 1984).

3.2.4 Genetics

Blood samples (n = 49) from the fish captured in Gilbert Bay in October 1996 (n = 12) and May 1997 (n = 37) were analysed by the Marine Gene Probe Laboratory, Dalhousie University (Ruzzante et al. in press). Variability in allele frequency in five microsatellite loci was analysed. The collection and processing of samples for DNA was conducted as described in Ruzzante et al. (1998). Polymerase Chain Reaction (PCR) amplification and analysis of these five loci was undertaken following Ruzzante et al. (1998). These five microsatellite loci were used in comparisons of the Gilbert Bay cod with inshore cod from Trinity Bay, as well as with offshore cod from several areas on the Northeast Newfoundland Shelf and the Grand Bank (Figure 3.1) (Ruzzante et al. in press). Estimates of subpopulation structure were obtained using F_{st} (Wright 1951) and R_{st} (Slatkin 1995). Genetic distances among populations based on a Stepwise Mutational Model were estimated using D_{sw} (Shriver et al. 1995). For comparison D_A, (Nei et al. 1983) a non-Stepwise Mutational Model estimate of genetic distance was also calculated. See Ruzzante et al. (in press) for details on the methods of the subpopulation structure and genetic distance analyses.

Blood samples (n = 87) from fish captured in Gilbert Bay in August 1996 (n = 50) and May 1997 (n = 37) were sent to the Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, BC, for a second, independent genetic analysis. Seven microsatellite loci were used in the analysis. These loci were different from those used by the Marine Gene Probe Laboratory (T. Beacham, Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, BC, personal communication). The analysis by Beacham was compared to the analysis by Ruzzante et al. (in press).

3.2.5 Morphometrics

Length-at-age and weight-at-age were compared for the cod captured in Gilbert Bay during 1996 and 1997 to determine if these samples could be pooled in subsequent morphometric analyses. Length and weight data from Gilbert Bay cod were then compared to cod collected inshore in 1995 in the Smith Sound area of Trinity Bay (n = 50), and to cod collected offshore by the Department of Fisheries and Oceans during annual research vessel surveys off Labrador during the years 1978-1995 (see Shelton et al. 1996). Mean lengths-at-age (n = 177) and mean weights-at-age (n = 177) from the research vessel survey were obtained from Tables 31a and 32b respectively, in Shelton et al. (1996). Although mean values were used, the means were not weighted by sample size, as the numbers caught-at-age were not provided by Shelton et al. (1996). No older fish (ages 8+ years) were caught in the later years of the survey (1992-1995). This may result in an unknown level of bias. Statistical analyses of morphometric data were undertaken with a general linear model routine (PROC GLM, SAS Inc. 1996). Since growth in length- and weight-at-age are nonlinear functions, regressions were performed

on $\log_{(10)}$ transformed data, and slopes were compared using an ANCOVA format within PROC GLM.

3.2.6 Factor analysis

Preliminary genetic analysis suggested the existence of two different groups of fish within the Gilbert Bay samples from 1996 and 1997, unrelated to year of capture. This differentiation appeared to be due to allele frequencies in just one of the five microsatellite loci analysed (D. Ruzzante, Danish Institute of Fisheries Research, Silkeborg, personal communication). In order to further investigate the possibility of population subdivision *within* Gilbert Bay, I conducted univariate and multivariate comparisons of the two possible groups of cod.

Univariate comparisons were undertaken through simple analysis of variance using the SAS routine PROC GLM (SAS Inc. 1996). A suite of morphometric variables was tested: length, age, sex, stage of maturity, wet weight, gonad weight, liver weight, gutted weight, thermal hysteresis, potential fecundity (subsample n = 15), and relative fecundity (subsample n = 15).

A multivariate analysis was undertaken to determine if the two possible groups identified genetically might be resolved through a simultaneous investigation of many morphometric measurements. In this analysis a factor analysis in principal components orientation (e.g Everitt and Dunn 1991) was conducted using MINITAB (MINITAB Inc. 1997). A total of eight variables were used: length, age, sex, stage of maturity, wet weight, gonad weight, liver weight, and thermal hysteresis.

3.3 Results

3.3.1 Sample description

Cod captured in August 1996 (Appendix A) were sampled from a depth range of 0 to 14.8 m, in water that ranged in temperature from 11.8 °C at the surface, to 4.6 °C at the bottom. The cod ranged in length from 38.5 to 69.5 cm, in weight from 0.57 to 3.64 kg (subsample n = 24), and 4 to 11 years in age. The cod sampled in October 1996 (Appendix B) were caught from a depth range of 7 to 20 m, with water temperatures from 6.3 °C at the surface to 7 °C at 20 m. The cod ranged in length from 44.5 to 65 cm, and in weight from 0.80 to 2.60 kg. The cod sampled in late May 1997 (Appendix C) were all caught in the upper 3 m of the water column. Water temperatures ranged from 4 °C at the surface to -0.7 °C at the bottom (approximately 10 m). Sampled cod ranged from 38 to 60 cm in length, from 0.49 to 1.99 kg in weight, and 4 to 15 years in age.

3.3.2 Antifreeze glycoprotein analysis

All of the 37 cod from the 1997 sample had antifreeze glycoproteins in their plasma, and almost 80 % exhibited thermal hysteresis levels exceeding 0.3 °C (S. Goddard, Antifreeze Protein Canada, St. John's, personal communication). Using the method of Goddard et al. (1994) the average thermal hysteresis level of 0.375 °C (SE = ± 0.015 °C) suggests that these cod had been exposed to sub-zero temperature seawater for a minimum of 60 days (Ruzzante et al. in press). Since sub-zero seawater temperatures are associated with inshore regions of the northeast Newfoundland and Labrador, these fish can be assumed to have overwintered in the Gilbert Bay area.

3.3.3 Fecundity

The subsample of mature females used in the analysis is small (15 of 37 fish), but two important results were evident in the data: the similarity in (*i*) fecundity-at-weight and the difference in (*ii*) fecundity-at-age of the Gilbert Bay sample relative to published values from other areas. While the female cod from Gilbert Bay were small, they had typical levels of oocyte production for their size. The potential fecundities as a function of weight of the Gilbert Bay females were comparable to the relationship reported by May (1967) for northern cod from the northern Grand Banks (Figure 3.3). The regression relationship reported in May (1967) was extrapolated to smaller weights as May (1967) did not sample any cod under 1.5 kg, and all of the females from the 1997 Gilbert Bay sample were below 1.5 kg in weight.

Due to the relatively slow growth rate of cod in Gilbert Bay, these cod have consequently a low fecundity-at-age relative to cod from other areas within the range of northern cod. Potential fecundity as a function of age is lower in Gilbert Bay than published estimates for Trinity Bay (Pinhorn 1984), and this difference increases with age (Figure 3.4).

3.3.4 Genetics

Analyses of genetic substructure using estimates of two statistics (F_{st} and R_{st}) revealed evidence of subpopulation genetic structure with both measures when undertaken over all five loci (Ruzzante et al. in press). Single locus estimates using the two statistics resulted in differing, but still statistically significant, outcomes. When measured with F_{st},

all five loci were responsible for the observed structure, whereas when measured with R_{st} three of the five loci were the origin of the structure (Table 3 of Ruzzante et al. in press).

Cod from Gilbert Bay differed significantly from all other samples of northern cod with both measures of genetic distance, D_{sw} and D_A. The distance estimates involving the Gilbert Bay sample were three- to fourfold greater in magnitude than those between any of the other northern cod samples when measured with D_A, and generally one order of magnitude greater when measured with D_{sw} (Table 4 of Ruzzante et al. in press,).

The second, independent genetic analysis rendered similar results despite using a different set of microsatellite loci (T. Beacham, Pacific Biological Station, Department of Fisheries and Oceans, Nanaimo, BC, personal communication). The sample from Gilbert Bay was the most distinctive of all inshore locations, and statistically different from all other areas. Samples collected from the bays of northeastern Newfoundland were not different from one another, but did show statistically significant genetic differentiation among most but not all offshore samples.

3.3.5 Morphometric analysis within Gilbert Bay

The length-at-age relationship of cod in Gilbert Bay was temporally stable over the two year duration of this study. When the comparison was limited to individuals used in the genetic analyses (1996, n = 48; 1997, n = 37), there was no significant difference between the slopes of the two curves ($F = 0.04$, $p = 0.8408$). Repeating the analysis using all of the available data from the two years (1996, n = 122; 1997, n = 37) did not reveal significant differences in length-at-age between years ($F = 1.13$, $p = 0.2901$) (Figure 3.5)

A similar analysis of weight-at-age could not be undertaken for cod used in the genetic analysis, as the genetic sample from 1996 was not weighed. However, those cod that were weighed in 1996 (n = 24) were not significantly different in weight-at-age (F = 1.36 , p = 0.2488) from cod sampled in 1997 (n = 36). Due to the lack of difference between years in length- and weight-at-age within Gilbert Bay, the 1996 and 1997 sampling years were pooled in subsequent morphometric comparisons of Gilbert Bay cod to northern cod from other areas.

3.3.6 Morphometric comparison among regions

Gilbert Bay cod were significantly smaller in length-at-age ($p < 0.0001$, $F_{1, 334} = 145.74$) and in weight-at-age ($p < 0.0001$, $F_{1, 235} = 78.78$) than offshore cod from the Northeast Newfoundland shelf off southern Labrador (Figures 3.6 and 3.7). Gilbert Bay cod were also smaller in length-at-age ($p < 0.0001$, $F_{1, 207} = 15.07$) and in weight-at-age ($p = 0.0036$, $F_{1, 108} = 8.87$) than cod from Trinity Bay (Figures 3.6 and 3.7). However, comparison of the samples from Trinity Bay and offshore of Labrador resolved no difference in either length-at-age ($p = 0.5464$, $F_{1, 225} = 0.36$) or weight-at-age ($p = 0.1516$, $F_{1, 225} = 2.07$). In addition, the weight-at-length relationship of cod in Gilbert Bay is similar to cod in Trinity Bay (Figure 3.8). The Gilbert Bay sample fit the (extrapolated) weight-at-length relationship estimated by regression for 267 cod caught in Trinity Bay in April 1995 (Hiscock 1997). The sample of cod (n = 50) from Trinity Bay in 1995 used in the morphometric and genetic analyses is a subsample of this larger data set. Thus, Gilbert Bay cod are not underweight compared to inshore cod of similar length, but rather appear to grow more slowly than cod from similar latitudes offshore and from Trinity Bay.

3.3.7 Multivariate analysis of Gilbert Bay cod

Preliminary genetic analysis suggested the possible existence of two different groups of fish within the Gilbert Bay samples from 1996 and 1997, unrelated to year of capture. A total of 49 cod were used in the genetic analysis; 12 cod from 1996 and 37 cod from 1997. Since the cod caught in 1996 were later released, the full suite of morphological measurements was not recorded. Therefore the subsequent morphological comparison of the two possible groups within Gilbert Bay identified by the genetic analysis used only 36 (one fish was not aged) of the 37 cod caught in 1997.

The possible existence of two groups within Gilbert Bay was not substantiated by an analysis of phenotypic characters. Comparison of single variables using oneway ANOVAs revealed no significant differences between the two identified groups (Table 3.1). In addition, factor analysis of a suite of morphometric variables did not support the existence of two groups of cod (Figure 3.9). The unrotated factor loadings and factor coefficients for the first three factors are presented in Table 3.2. The three weight variables were relatively highly correlated ($0.514 \leq r \leq 0.710$), therefore gonad and liver weights were excluded and the analysis was undertaken again using six variables. The outcome of this second analysis is provided in Table 3.3 and Figure 3.10. The subsequent exclusion of sex in a third analysis of the five remaining variables resulted in an improvement in the variance explained (Table 3.4 and Figure 3.11). This was the only reason for the exclusion of this variable. In the three tests, the first two components explained 64-70% of the variance, and the first three components explained 79-89% of the variance.

3.4 Discussion

Atlantic cod that inhabit Gilbert Bay, Labrador were genetically distinguishable from other inshore (Trinity Bay) and from adjacent offshore (Labrador) components of northern cod. In addition, cod in Gilbert Bay grew more slowly and therefore demonstrate lower length- and fecundity-at-age relationships, thus their capacity for production and recruitment was lower than northern cod from elsewhere within the population's range. These results lead me to conclude that: (*i*) a subpopulation of northern cod exists in Gilbert Bay, and (*ii*) thus the subpopulation located in Trinity Bay is not a unique phenomenon.

Temperature is responsible for the greatest proportion of variation in growth for Atlantic cod throughout their range (Brander 1994), therefore the relatively small size-at-age for Gilbert Bay cod suggests that they experience lower temperatures than any other subpopulation of northern cod (offshore and inshore). The observed levels of thermal hysteresis and the inferred production of antifreeze glycoproteins are consistent with the above suggestion. These results indicate that the cod from Gilbert Bay overwinter in subzero inshore waters (temperature below the seasonal thermocline is subzero year-round; unpublished data) and do not migrate offshore as do the majority of northern cod. However, the Gilbert Bay cod assessed for antifreeze activity were collected on May 30 and June 1 from the surface layer that had a shallow (3 m) thermocline above which temperatures ranged from 2.5 °C to 5.8 °C and below which temperatures were consistently < 0 °C. The time of year, local temperature and the proposed pattern of antifreeze production in cod (Fletcher et al. 1987) lead me and my colleagues (Ruzzante et

al. in press) to conclude that the antifreeze levels in the cod were decreasing from thermal hysteresis values 0.5 °C or greater. Such values are attained after greater than 75 days of exposure to subzero temperatures and are maintained as long as the fish remain in subzero water (Goddard et al. 1994). Antifreeze is lost from the blood plasma at a rate proportional to the temperature of the fish: the biological half-life is 15.6 ± 5 days at 5 °C, 37.3 ± 2.9 days at 1 °C and > 100 days at < 0 °C (Fletcher et al. 1987). Incursions of cod into the warmer surface layer in Gilbert Bay would initiate antifreeze clearance and provide the range of thermal hysteresis estimates observed (Ruzzante et al. in press). These observations and their interpretation are consistent with those reported for overwintering cod in Trinity Bay (Goddard et al. 1994; Ruzzante et al. 1996).

Sonic tagging studies recently conducted in Gilbert Bay (J. Green and J. Wroblewski, Memorial University of Newfoundland, St. John's; unpublished data) show that cod not only overwinter in Gilbert Bay, they remain active in subzero temperatures throughout the winter. Observations of their reproductive stages (Appendix C) indicate these cod would spawn in late spring and early summer as do cod that overwinter in Trinity Bay (Smedbol and Wroblewski 1997; Smedbol et al. 1998) and as do cod from Ogac Lake, Baffin Island (Patriquin 1967). Therefore cod spawning within Gilbert Bay occurs much later than offshore spawning (January to March; see Myers et al. 1993), suggesting temporal barriers to gene flow due to environmental effects between inshore cod (both from Gilbert Bay and Trinity Bay) and offshore northern cod. Such limitations to gene flow meet one of the requirements for the existence of metapopulation dynamics:

semi-isolation of subpopulations, with few migrants exchanged, resulting in asynchronous (independent) subpopulation dynamics.

Other lines of evidence for year-round presence of cod within Gilbert Bay include the existence of a historical (at least since 1973) longline, trap, and gillnet fishery in the inner reaches of the bay in the early spring, before the offshore-spawning/inshore-migrating cod arrive at their inshore feeding grounds (Powell 1987). Such a "two-stage" fishery pattern is consistent with that reported for other embayments in Newfoundland (Lilly 1996).

The relatively high and significant levels of population structure estimated in the microsatellite DNA analysis undertaken by Ruzzante et al. (in press) indicate that there are important barriers to gene flow among the five population components that include two inshore subpopulations (Gilbert Bay and Trinity Bay) and three offshore cod aggregations from the Northeast Newfoundland Shelf and the Grand Bank region (Figure 3.1). Estimates of D_A and D_{SW} genetic distance between any pairwise combination of these five population components indicate that cod from Gilbert Bay are the most genetically divergent of the five components because the estimates are three- to ten-fold larger when Gilbert Bay cod are involved than when they are not (Ruzzante et al. in press). This illustrates that Gilbert Bay cod are more reproductively isolated than are the other identified subpopulations of northern cod.

The investigations presented in this chapter identify three important characteristics of the Gilbert Bay subpopulation in relation to the dynamics of the (proposed) northern cod metapopulation. First, this subpopulation is small relative to other northern cod

subpopulations in terms of geographic extent. Small population size allows genetic drift in neutral markers. Second, the relatively high degree of genetic isolation may indicate that the persistence of this subpopulation is less influenced by immigration (the "rescue effect"; Hanskii 1991) compared to other subpopulations. Third, the Gilbert Bay subpopulation experiences relatively slow population growth, as evidenced by slow individual growth and low fecundity-at-age. From these three characteristics I conclude that the Gilbert Bay subpopulation is likely to exhibit a higher base probability of extinction in a metapopulation framework than other northern cod subpopulations. Small population size, slow growth and reduced fecundity-at-age make Gilbert Bay cod particularly vulnerable to the effects of commercial fishing.

Table 3.1. Oneway ANOVA comparisons of single variables between the two possible groups (n = 10 and n = 26) of cod within the sample from Gilbert Bay in 1997, as identified by microsatellite allele frequency.

Morphological trait	F statistic	p - value
Length (cm)	0.2	0.657
Age (years)	1.2	0.282
Stage of maturity (six stages; Appendix C)	0.32	0.578
Wet weight (kg)	0.17	0.682
Gonad weight (g)	0.1	0.752
Liver weight (g)	0.61	0.438
Gutted weight (g)	0.12	0.727
Thermal hysteresis (°C)	0.76	0.388
Potential fecundity (oocytes)	1.11	0.312
Relative fecundity (oocytes·g^{-1})	1.25	0.284

Table 3.2. Principal component factor analysis of Gilbert Bay cod sampled in 1997 conducted with eight morphometric variables. Factor loadings are presented in Figure 3.12.

Variable	Unrotated factor loadings			Factor score coefficients		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Length (cm)	-0.923	-0.270	-0.064	-0.272	-0.158	-0.059
Age (year)	-0.527	-0.242	0.498	-0.155	-0.142	0.464
Wet weight (kg)	-0.939	-0.253	-0.017	-0.277	-0.148	-0.016
Sex	-0.192	0.816	-0.247	-0.056	0.477	-0.230
Stage of maturity	-0.226	0.809	0.026	-0.066	0.473	0.024
Gonad weight (kg)	-0.811	0.261	-0.008	-0.239	0.153	-0.007
Liver weight (kg)	-0.798	0.061	-0.218	-0.235	0.036	-0.203
Thermal hysteresis (°C)	0.041	-0.350	-0.844	0.012	-0.205	-0.786
Variance	3.3933	1.7109	1.0737			
% Variance	0.424	0.214	0.134			

Table 3.3. Principal component factor analysis of Gilbert Bay cod sampled in 1997 conducted with six morphometric variables. Factor loadings are presented in Figure 3.13.

Variable	Unrotated factor loadings			Factor score coefficients		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Length (cm)	0.967	0.037	0.146	0.416	0.025	0.143
Age (year)	0.671	0.022	-0.376	0.289	0.014	-0.366
Wet weight (kg)	0.954	0.042	0.078	0.410	0.028	0.076
Sex	-0.139	0.786	0.293	-0.060	0.518	0.285
Stage of maturity	0.058	0.858	0.136	0.025	0.565	0.133
Thermal hysteresis (°C)	0.079	-0.401	0.868	0.034	-0.264	0.846
Variance	2.3247	1.5188	1.0264			
% Variance	0.387	0.253	0.171			

Table 3.4. Principal component factor analysis of Gilbert Bay cod sampled in 1997 conducted with five morphometric variables. Factor loadings are presented in Figure 3.14.

Variable	Unrotated factor loadings			Factor score coefficients		
	Factor 1	Factor 2	Factor 3	Factor 1	Factor 2	Factor 3
Length (cm)	0.968	-0.067	-0.148	0.418	-0.056	-0.160
Age (year)	0.671	0.088	0.518	0.290	0.074	0.561
Wet weight (kg)	0.954	-0.021	-0.109	0.412	-0.018	-0.118
Stage of maturity	0.109	0.727	-0.621	0.047	0.606	-0.672
Thermal hysteresis (°C)	0.066	-0.811	-0.486	0.028	-0.676	-0.525
Variance	2.3151	1.1997	0.9243			
% Variance	0.463	0.240	0.185			

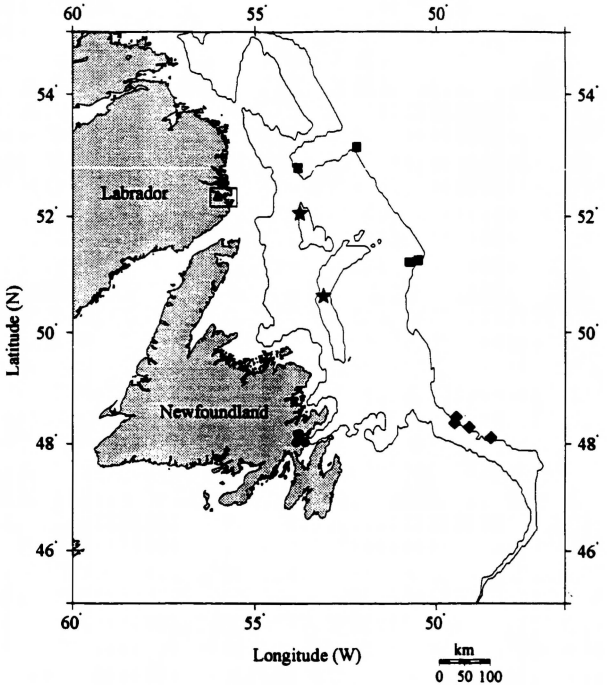

Figure 3.1. Locations where northern Atlantic cod were collected for genetic analysis: Gilbert Bay (▲), NORTH (■), SAND (★), SOUTH (◆), and Trinity Bay (●). The box provides the location and extent of the Gilbert Bay study area presented in Figure 3.2 (after Ruzzante et al. in press).

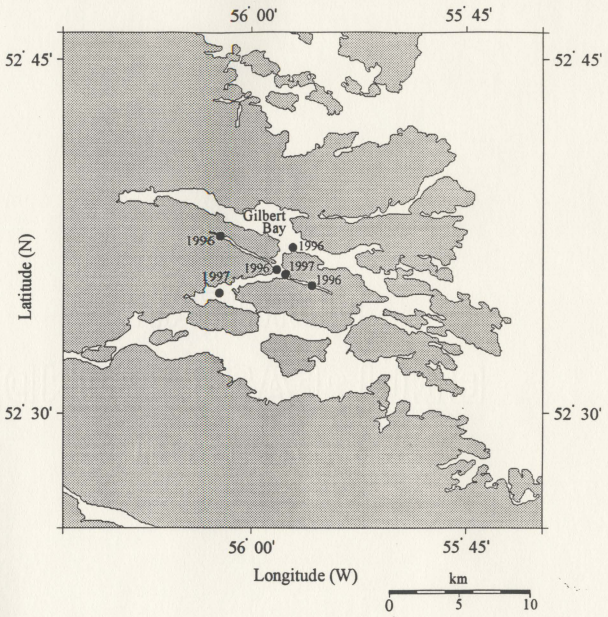

Figure 3.2. Locations in Gilbert Bay where samples were collected in August 1996 (n = 122), October 1996 (n = 12), and May 1997 (n = 37). Note the nearly land-locked geography of Gilbert Bay.

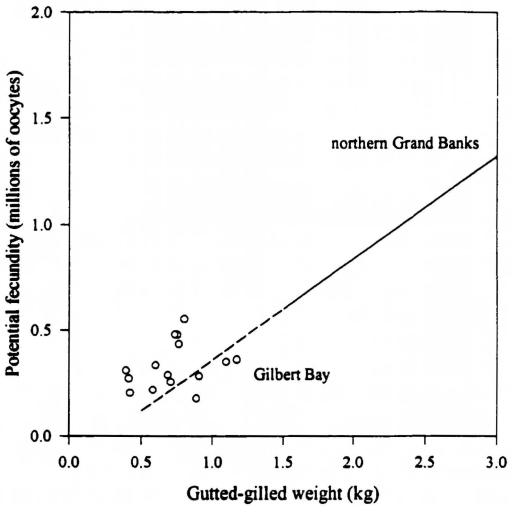

Figure 3.3. Potential fecundity for Gilbert Bay cod (n = 15) sampled in May 1997 (circles) plotted against gutted-gilled weight. The fecundity-weight relationship for cod from the northern Grand Banks reported by May (1967) is given by the solid curve, and extrapolated (dashed curve) to the lower weights of the Gilbert Bay sample.

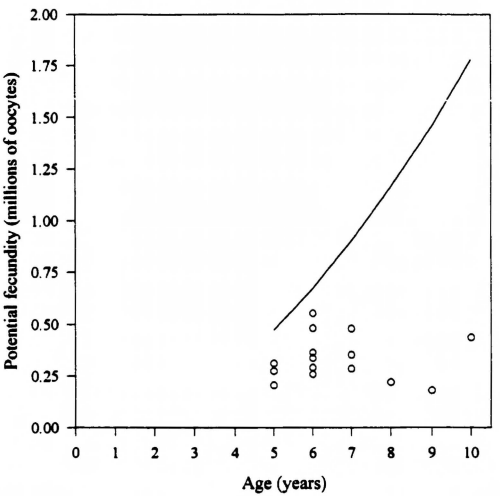

Figure 3.4. Potential fecundity for Gilbert Bay cod (n = 15) sampled in May 1997 (circles) plotted against age. The fecundity-age relationship for Trinity Bay cod reported by Pinhorn (1984) is given by the solid curve (after Ruzzante et al. in press).

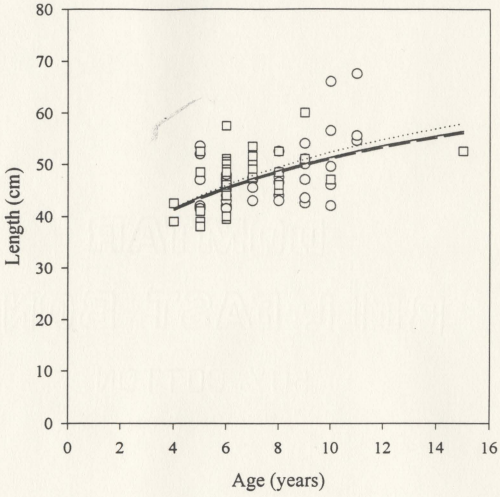

Figure 3.5. Length-at-age relationships for the subsamples of cod caught in 1996 (circles, n = 48) and 1997 (squares, n = 36) used in the genetic analysis. Regression lines: 1996 (dashed line, Length = $29.885Age^{0.232}$); 1997 (dotted line, Length = $29.448Age^{0.250}$); all cod caught in 1996 and 1997 (solid line, Length = $33.238Age^{0.183}$, n = 159).

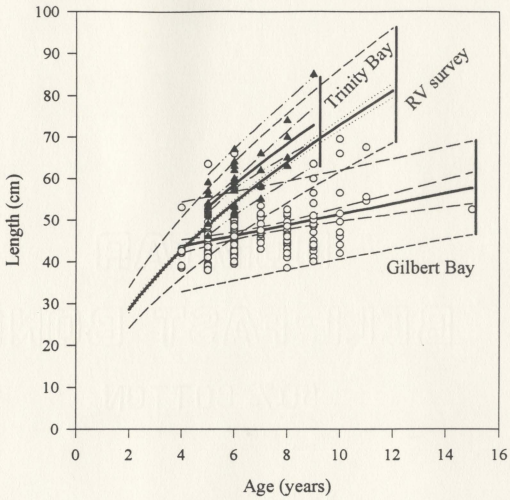

Figure 3.6. Length-age relationship for Gilbert Bay cod (open circles, n = 159) sampled in 1996 and 1997 compared to Trinity Bay cod (filled triangles, n = 50) sampled in April 1995 and to the research vessel (RV) survey in NAFO Division 2J. For each sample, the solid, heavy curve is the regression relationship; the inner lines around the regression line are the upper and lower 95% confidence limits (CIs) for the population estimates; and the outer lines are the 95% CIs for individuals. The survey data for 2J were obtained from Table 31a in Shelton et al. (1996).

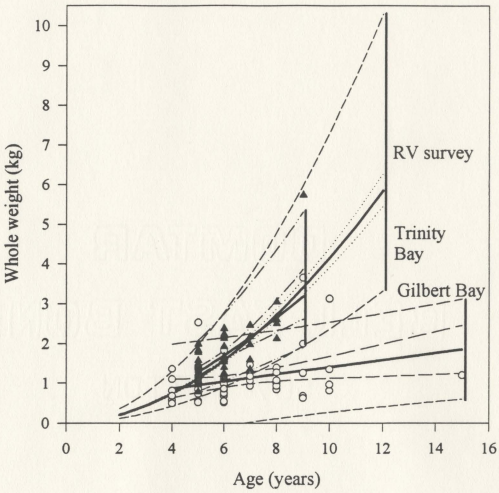

Figure 3.7. Weight-age relationship for Gilbert Bay cod (open circles, n = 60) sampled in 1996 and 1997 compared to Trinity Bay cod (filled triangles, n = 50) sampled in April 1995 and to the research vessel (RV) survey in NAFO Division 2J. For each sample, the solid, heavy curve is the regression relationship; the inner lines around the regression line are the upper and lower 95% confidence limits (CIs) for the population estimates; and the outer lines are the 95% CIs for individuals. The survey data for 2J were obtained from Table 32b in Shelton et al. (1996).

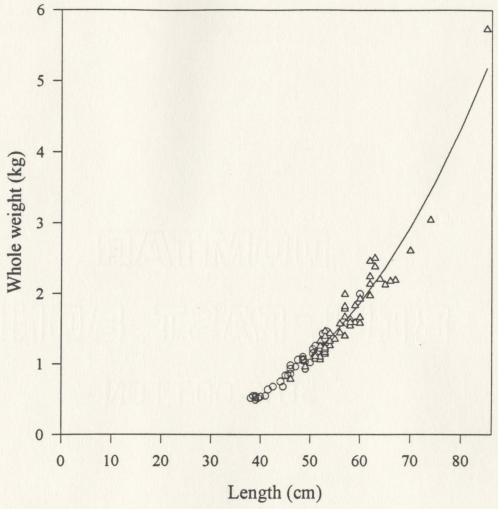

Figure 3.8. Weight-length relationship for Gilbert Bay cod (n = 37) sampled in May 1997 (circles), compared to Trinity Bay cod (n = 267) sampled on 24 April 1995 (curve expressed by $W = 1.15 \times 10^{-2} L^{2.93}$; $r^2 = 0.91$, $p < 0.0005$). The triangles represent the subsample of 50 cod from the sample of 267 cod from Trinity Bay that was used in the morphometric analysis.

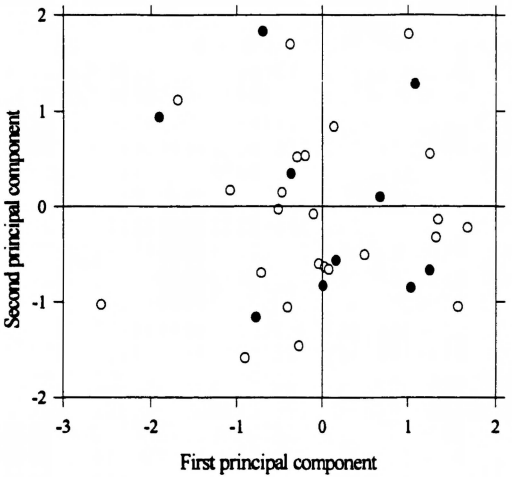

Figure 3.9. Scores plot of the first two principal components generated from a factor analysis incorporating eight morphometric variables from the Gilbert Bay cod sample collected in May, 1997. Members of the two putative subgroups derived from microsatellite genetic analysis are identified by hollow or filled circles.

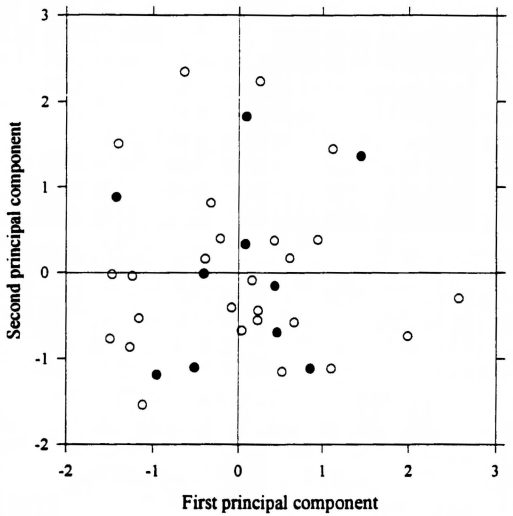

Figure 3.10. Scores plot of the first two principal components generated from a factor analysis incorporating six morphometric variables from the Gilbert Bay cod sample collected in May, 1997. Members of the two putative subgroups derived from microsatellite genetic analysis are identified by hollow or filled circles.

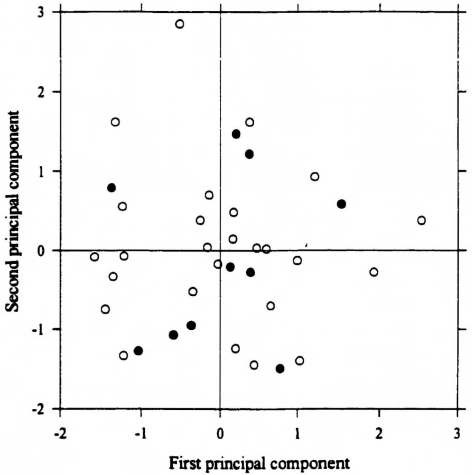

Figure 3.11. Scores plot of the first two principal components generated from a factor analysis incorporating five morphometric variables from the Gilbert Bay cod sample collected in May, 1997. Members of the two putative subgroups derived from microsatellite genetic analysis are identified by hollow or filled circles.

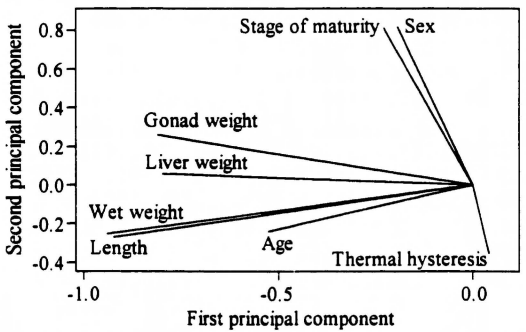

Figure 3.12. Factor loadings from a factor analysis in principal components orientation incorporating eight morphometric variables from the Gilbert Bay cod sample collected in 1997.

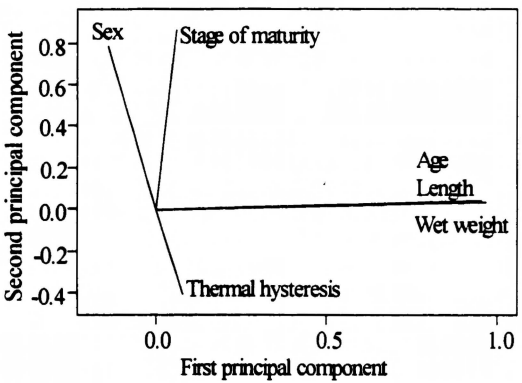

Figure 3.13. Factor loadings from a factor analysis in principal components orientation incorporating six morphometric variables from the Gilbert Bay cod sample collected in 1997.

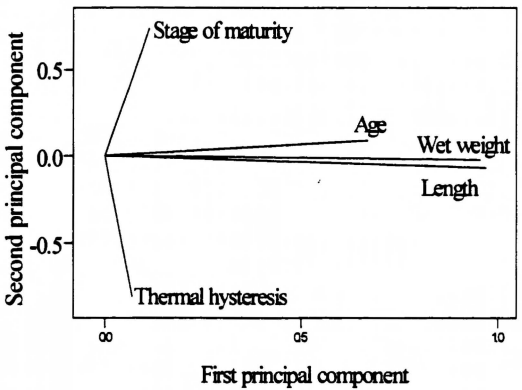

Figure 3.14. Factor loadings from a factor analysis in principal components orientation incorporating five morphometric variables from the Gilbert Bay cod sample collected in 1997.

Chapter 4: A metapopulation model of northern cod

4.1 Introduction

In the previous chapters I reviewed evidence for spatial structure in northern cod during the breeding season. I contend that this structure can be interpreted as subpopulation structure in northern cod. In Chapter 1 I reviewed previous studies that suggested the existence and location of subpopulations associated with major offshore banks. Chapters 2 and 3 presented recent, detailed evidence supporting the existence of local subpopulations in the coastal areas of Newfoundland (Trinity Bay) and Labrador (Gilbert Bay). These subpopulations are at least semi-isolated from the rest of northern cod as indicated by genetic differentiation among areas. While mixing of individuals from different subpopulations occurs during the feeding season, these subpopulations segregate during the spawning season. Mechanisms responsible for this isolation may include local retention of eggs and larvae, spatial separation of spawning sites (with little straying of adults), and differences in the timing of the local spawning intervals (temporal separation). From evidence contained in published studies, together with my recent collaborative investigations in Trinity and Gilbert Bays, I conclude that northern cod can be viewed as a metapopulation, and thus the spatial dynamics of this stock complex may be adequately modelled using metapopulation theory.

In this chapter I use the basic model of Levins (1970) to explore, via simulations, the spatial dynamics of northern cod. I modify the Levins model and redefine some of its

components in order to apply the model to the particular situation presented by northern Atlantic cod. The objectives of this modelling investigation are: 1) to examine the spatial dynamics of this metapopulation on scales of years, as evidenced in the occupancy rate of known major spawning areas; 2) to derive first approximations of the values of the model's colonization and extinction parameters; 3) to examine how the metapopulation may behave during periods of declining occupancy; 4) to predict recovery times from relatively low to high states of occupancy under various parameter values.

4.2 The model

The model for northern cod will be derived from the basic metapopulation equation as presented by Levins (1970). Recall from Chapter 1 that:

4.1) $$\frac{dP}{dt} = mP(1 - P) - eP$$

where P is the fraction of habitat patches occupied at time t, m is the "colonization" parameter, and e is the "extinction" parameter. The rate of colonization of new (empty) habitats is assumed to be proportional to P, the fraction of occupied habitats, and to $(1 - P)$, the fraction of unoccupied habitats.

In the model for northern cod, P represents the proportion of suitable *spawning areas* that are occupied, analogous to the proportion of occupied *habitat patches* in models for terrestrial species. In terms of my hypothesis, one important assumption is

made: an individual breeds in only one of the designated areas during a single spawning season. The particular spawning area in which an adult spawns may differ between years, but the individual must spawn in only one during a single spawning season.

4.2.1 Parameter estimation

I estimate colonization and extinction rates for northern cod subcomponent areas as follows. The values of the colonization and extinction parameters in the model are affected by a number of biotic and abiotic processes in a species specific manner. A number of the mechanisms and species characteristics that influence northern cod metapopulation dynamics are listed in Table 4.1. These factors are included because they affect the possible numbers of dispersers available for colonization and the ability of individuals to reach other subpopulations and unoccupied habitat (spawning areas). Populations with a relatively high intrinsic rate of natural increase (r) have the ability to produce numerous migrants. The mobility (e.g Lear and Green 1984; Wroblewski et al. 1995) of adult cod provide migrants with the ability to reach any spawning area from one season to the next. While cod prefer particular prey and thermal regimes (eg. Rose 1993; Taggart et al. 1994), they consume a wide variety of prey species and are found inhabiting a broad range of ocean temperatures. Numerous studies have reported the importance of the physical structure of the environment, such as currents, in the spatial and temporal dynamics of marine fishes (e.g. MacCall 1990). Physical processes influence the dispersal (or retention) of propagules, the location migration pathways, and productivity of the ecosystem (e.g. Sinclair 1988). Climate and weather, while operating on different time scales, produce both direct and indirect effects on the metapopulation (Cushing 1982).

Environmental conditions such as water temperature can affect cod directly, or indirectly by influencing the dynamics of prey species (e.g. Rose 1993).

I propose that with the lack of direct studies of individual subpopulations, reasonable parameter estimates for the simple model may be derived from an analysis of cod life history on appropriate time scales. Metapopulation dynamics concern the turnover of subpopulations rather than individuals. Metapopulation models are usually solved on generational time scales. However, reproduction in Atlantic cod is age-structured, with a number of mature age-classes contributing to reproduction each year. Thus an annual time scale may be more appropriate, or at least more manageable considering that age-at-maturity can change over time (Taggart et al. 1994; Morgan and Brattey 1997).

4.2.1.1 The extinction parameter

Individual cod can survive to a considerable age, with one cod as old as 29 years recorded (Scott and Scott 1988). However, cod very rarely exceed 25 years of age. In the stock assessment process, an annual survivorship of 80% (i.e. 20 % natural mortality) is assumed for sexually mature year-classes (Shelton et al. 1996). I use the maximum individual lifespan to arrive at appropriately scaled rates of extinction (e) in the model. A spawning area will not become "extinct" (unoccupied) unless spawning has been unsuccessful for the entire lifespan of the youngest individuals in the subpopulation during the period of spawning failure. In addition, there must be no substantial immigration into the subpopulation (no rescue effect). The period from birth to death of the youngest

individuals can be no longer than the maximum individual lifespan of 29 years. Therefore, the extinction rate is per 1 maximum lifespan, so e can be no lower than:

4.2) $$e = \frac{1}{29\ years}$$

or $e = 0.03\ yr^{-1}$.

The conditions I have listed above of no rescue effect and successive years of complete spawning failure are unlikely to commonly occur, given the historic spatial spread and age structure of this population (> 10^9 adults aged 6+ years in the early 1960s; Taggart et al. 1994).

4.2.1.2 The colonization parameter

An estimate of the colonization parameter m is more difficult to determine. I have used literature sources to estimate historic values of P, and derived a value for m knowing P and e. During the late 1800s and early 1900s, the commercial fishery was prosecuted across the entire latitudinal range of northern cod, from the northern area of the Grand Bank in the south to Cape Chidley at the northern tip of Labrador (Lear and Parsons 1993). However, during its history the northern cod fishery has exhibited substantial variation in total catch and in catch per unit effort at regional (i.e. local subpopulation) spatial scales (Lear and Parsons 1993, Figures 2 and 3; Hutchings and Myers 1995, Figure 2). In addition, other populations of Atlantic cod have also shown such variation, to the point of local fishery collapse (e.g. Jónsson 1994; Øiestad 1994). Thus I assumed that prior to intensive, large scale harvesting of the stock, at least 90 % of the major spawning

areas were occupied ($P = 0.9$). I then solved for the value of m using values of $P = 0.9$ and $e = 0.03$ yr^{-1} under equilibrium conditions. Recall from Chapter 1 that at equilibrium:

4.3) $$\hat{P} = 1 - \frac{e}{m}$$

Therefore, using the above parameter values $m = 0.3$.

Another important characteristic of the northern cod metapopulation model is the manner in which empty spawning areas are recolonized. I contend that the agents of colonization of unoccupied areas may be groups of adult cod, drifting eggs and larvae, or both. Recolonization of habitat to the north against the mean current flow is probably accomplished by adults (Figure 1.2c). Southern areas may be colonized by either adults or drifting eggs and larvae. Colonization by adults is achieved by groups of fish rather than individuals. Spawning areas are occupied by sexually mature individuals, and prespawning and spawning adults tend to aggregate in shoals; relatively large shoals in offshore areas (e.g. Rose 1993), and considerably smaller shoals inshore (e.g. Rose 1996; Smedbol and Wroblewski 1997). If recolonization was to occur through the immigration to an unoccupied area by just a few mating pairs of adults, the survivorship of offspring would have to be high to establish a resident subpopulation. Shoals of adult fish often travel long distances (Rose et al. 1995; Wroblewski et al. 1995) and may end up spawning in new areas. An example of these movements (relocations) of such shoals may be the aggregation detected in Smith Sound, Trinity Bay in April 1995 (see Chapter 2; Rose 1996; Smedbol et al. 1998) and monitored in the Sound on several occasions thereafter.

4.2.1.3 The effect of fishing

The northern cod population has been exposed to some level of harvest, either subsistence or commercial fishing, for approximately 500 years (Hutchings and Myers 1995). The impact of fishing on the spatial dynamics of northern cod could be significant. While fishing mortality in areas within the range of northern cod has been estimated (Myers et al. 1997a), at present no studies have documented fishing mortality at a suitable geographic and temporal scale to be of direct use in the model. Therefore, without direct estimates of the fishing mortality, the influence of harvesting must be indirectly incorporated into the model. I accomplish this by separating the extinction parameter e into two terms, such that:

4.4) $$e = e_N + e_F$$

where e_N is the "natural" extinction rate in the absence of fishing, and e_F is the extinction rate due to harvest. The extended Levins model for northern cod then becomes:

4.5) $$\frac{dP}{dt} = mP(1 - P) - (e_N + e_F)P$$

If $e_F = 0$ yr^{-1}, P will be close to 1. As the value of $e_N + e_F$ approaches m, the metapopulation begins to decline in spatial range as the number of occupied areas decreases. Since during the historical record northern cod has only recently (the 1960s)

undergone a substantial decline, the historical effect of fishing on the extinction parameter must have been relatively small ($e_F << m$).

While I have chosen values for the colonization and extinction parameters based on several assumptions discussed above, model runs were executed wherein these values were varied in order to determine the possible effect of incorrect parameter estimation on the predictions derived from the model. The first set of model runs was undertaken with the extinction parameter held constant at $e = 0.03$ yr^{-1} as conceived from the occupancy limitations due to maximum life expectancy. In the second set of model runs, the colonization parameter was held constant at $m = 0.3$ yr^{-1}, as determined from Equation 4.3 and the assumption of historic equilibrium proportion of occupancy at $P \approx 0.9$. This procedure allowed for the analysis of the effect of fish harvesting on the rate of extinction of occupied spawning areas. I determined the fishing effect (e_F) on northern cod through the comparison of model output under various levels of e to the actual recent collapse of the northern cod population.

4.3 Results

4.3.1 Equilibrium solutions of the basic Levins metapopulation model

Equilibrium solutions of the Levins model (Equation 4.3) for various values of the colonization (m) and extinction (e) parameters are presented in Figures 4.1 and 4.2. The proportion of occupied spawning areas increases from zero as the colonization parameter exceeds the extinction parameter. If m is twice the value of e, then half of the suitable

areas will be occupied. If m is three times the value of e, then 67 % of the areas will be utilized, and 90 % of the areas are used if m is 10 times larger than e.

4.3.2 Model dynamics with an extinction parameter value of $e = 0.03$ yr^{-1}

Model output for an extinction parameter value of 0.03 yr^{-1}, under a range of colonization rates and initial occupancies is presented in Figure 4.3. Several generalizations are possible from the analysis. First, irrespective of the colonization parameter value, the time to reach equilibrium decreases as the initial area occupancy increases. Second, as the colonization parameter is reduced, the time to reach equilibrium increases for all initial values of the proportion of occupied areas. Third, decreasing the colonization parameter value results in a concomitant decrease in the proportion of areas occupied at equilibrium. As a result, a low rate of colonization relative to the extinction rate has a dual effect on the spatial dynamics of the metapopulation: the time period required to reach equilibrium is extended and the proportion of occupied areas at equilibrium is reduced.

4.3.3 Model dynamics with a colonization parameter of $m = 0.3$ yr^{-1}

Model output for a colonization parameter value of 0.3 yr^{-1}, under a range of extinction rates and initial occupancies is presented in Figure 4.4. The effect of increasing the extinction rate is comparable, but not identical, to the effect of deceasing the colonization rate. Similar to the result of falling m values, the time period necessary to reach equilibrium increases as the initial occupancy decreases, regardless of the magnitude of the extinction parameter. In addition, rising values of e effect a decrease in the proportion of occupied areas at equilibrium (Table 4.2). However, as e is increased, the

time required to reach equilibrium does not lengthen as quickly as under a regimen of decreasing colonization rate (Figures 4.3 and 4.4).

Decreasing both m and e by an order of magnitude results in the same equilibrium P, but the time period to reach equilibrium becomes unrealistically long (order 50 years).

4.4 Discussion

In this modelling study, I have derived values for the colonization and extinction parameters that are first approximations of the actual values, when considering the model output in the context of recent and historical spatial dynamics of northern cod. I have hypothesised that in the absence of a commercial fishery, northern cod usually occupy most, if not all of the effective spawning areas. This supposition seems to be supported by an analysis of the spatial spread and pattern during the history of the commercial fishery (Hutchings and Myers 1995). The metapopulation model I have constructed can be used to develop predictions of the spatial dynamics of this population during periods of population collapse and subsequent recovery. Population collapse may have natural (e.g. environmental) and anthropogenic (unsustainable levels of harvesting) causes, together with possible interactive effects between these factors. Given that overfishing is generally accepted as the primary cause of the recent collapse of northern cod (e.g. Hutchings and Myers 1994), the model can be used to predict how the spatial dynamics of the metapopulation will behave during the decline, and how various levels of fishing intensity may affect the spatial recovery of this population, keeping in mind that fishing effects on abundance are included only indirectly in the metapopulation model.

4.4.1 Model parameterization of the effect of fishing: e_F

The result of modifying the extinction parameter to include the effect of harvesting on the stock is a decrease in the number of occupied spawning areas at equilibrium (Figure 4.4). As one would expect, the decline in the number of occupied spawning areas is accentuated under increasing rates of extinction. Following the implementation of harvesting, the new equilibrium proportion of occupied areas is attained in 10-20 years, depending on the intensity of fishing (Figure 4.4).

The prediction that I would draw from this analysis is that under prolonged and intensive fishing, the distribution of the northern cod metapopulation during the spawning season would be reduced as some of the aggregations (subpopulations) associated with particular spawning locations decline to extinction due to sustained overexploitation. The model cannot predict what will happen to individual subpopulations, only that the number of suitable areas occupied will be reduced. If harvesting does not increase to the point where the persistence of the entire metapopulation is threatened, the system will reach a new equilibrium, albeit with fewer subpopulations than prior to exploitation.

This prediction from the model is supported by the changes in distribution of northern cod following the implementation of new gear technology in the commercial fishery. The unsustainability of inshore catch rates in both the early (Hutchings and Myers 1995) and recent fishery provides one piece of evidence (Hutchings and Myers 1994). Myers et al. (1997a) used mark-recapture data to estimate that since the 1940s exploitation rates of inshore components of northern cod have been very high, with instantaneous fishing mortalities exceeding F = 1 (> 63% mortality per year) in the 1980s

and early 1990s. At the least, these inshore subpopulations had a very low probability of increasing in abundance during this period under such high levels of fishing mortality. Currently, only a few known spawning areas are occupied by northern cod, including Trinity and Gilbert Bays (Chapters 2 and 3), the northern Grand Bank (e.g. Shelton et al. 1996), and Hawke Saddle, on the southern edge of Hamilton Bank (Figure 1.3; G. Rose, Fisheries Conservation Chair, Memorial University of Newfoundland, personal communication).

4.4.2 Model predictions for recolonization by northern cod

Since the summer of 1992 the northern cod stock complex has been under a commercial fishing moratorium. A limited commercial fishery will be permitted in 1999. Metapopulation models of northern cod could be used to provide insight as to how this population might recover, in terms of the re-occupation of currently empty spawning areas within the metapopulation's historical geographic range. When and how might these empty areas be recolonized? In the metapopulation model I constructed for northern cod, initial conditions of low occupancy (P) result in extended recovery intervals (Figure 4.4). Essentially, the lower the initial occupancy of spawning areas (the current situation for northern cod), the longer the time period required to return to an equilibrium proportion of occupied areas. This delay is enhanced by elevating the value of the extinction parameter (e) to simulate increasing levels of harvest (fishing mortality). For instance, at an initial occupancy proportion of $P = 0.1$, the length of time to return to equilibrium occupancy increases from 27 to 40 years as the extinction parameter is raised from $e =$

0.03 to 0.15 yr^{-1} (Table 4.2). In addition, the metapopulation will reach equilibrium with a lower proportion of areas occupied.

I interpret the model simulations as providing the prediction that if adult aggregations function in colonization of unoccupied spawning areas, commercial fishing will inhibit the spatial recovery of the northern cod metapopulation. The simulations imply two possible effects of fishing upon metapopulation recovery: (1) the length of time required for recovery to equilibrium proportions of area occupancy will increase relative to the amount of time needed under a moratorium, and (2) the proportion of spawning areas used by northern cod at equilibrium will be lower than the proportion occupied by this metapopulation in the absence of commercial harvesting.

I hypothesize that fishing affects the rate of spatial spread (recovery) by limiting or removing excess individuals from occupied areas, thereby preventing these individuals from serving as colonizing immigrants to currently unoccupied areas. Recolonization would therefore be more dependent on the straying (drift) of eggs and larvae, which is much more likely to occur in the direction of the mean current flow (south of the spawning location), rather than against the mean current (north of the spawning area).

Support for these model predictions can be obtained from documented changes in northern cod distribution. As an example, intense overfishing from 1965-1969 decimated the subpopulations associated with Saglek and Makkovik Banks off northern Labrador (Figure 1.3) (NAFO Divisions 2G and 2H). These subpopulations have yet to recover, and commercial catches in these areas have remained low since the early 1970s (Lear and Parsons 1993). In fact, the lack of recovery in these areas is the reason cited for their

exclusion from the *management* unit of northern cod, designated as NAFO Divisions 2J3KL, which includes the range from Hamilton Bank in the north to the northern section of the Grand Bank in the south (Pinhorn 1976), even though Saglek and Makkovik Banks were considered a northern component of the northern cod stock complex (Lear and Parsons 1993). This example also demonstrates the lack of synchrony in the dynamics of the constituent subpopulations, which is one of the defining characteristics of metapopulation structure.

An examination of the dynamics of northern cod following the implementation of the 200 mile Economic Exclusion Zone in 1977 by the Government of Canada also provides some evidence for model predictions of a spatial recovery. Northern cod has been fished at relatively high intensities since the introduction of offshore otter trawlers into the fishery (Hutchings and Myers 1994). The metapopulation model predicts a decrease in the number of occupied spawning areas with increased total rate of extinction e, where e includes the simulated influence of fishing (Equations 4.5 and 4.6). Following the institution of the 200 mile limit, northern cod exhibited some recovery in abundance (e.g. Hutchings and Myers 1994), however most of these potential colonizers were gone by the late 1980s, harvested by the commercial fishery, thus precluding the possible re-occupation of empty spawning areas in the northern section of the metapopulation's geographic range.

The model presented in this chapter is sensitive to changes in the extinction parameter (Figure 4.4). For a recovery to occur, time is needed for currently occupied areas to increase in abundance to the point where enough adults have been produced to

form potential colonizing aggregations. These aggregations then reoccupy surrounding, empty spawning areas. If the model is realistic, then any fishing on the remaining subpopulations would be detrimental, since harvesting removes potential colonizers. Local subpopulations must exhibit more than just existence. In order for unoccupied areas to be colonized, these subpopulations must be fully occupied to produce: (1) the *surplus* of adults necessary to form recolonizing aggregations, and (2) the quantity of eggs required for successful recolonization by larval drift. The production of adults is especially necessary for the recolonization of the more northerly spawning areas, as these locations do not receive input of eggs and larvae from drift, which occurs in a southerly direction.

4.4.3 Comparison of model predictions with current field observations

At present, seven years have passed since northern cod was placed under a commercial fishing moratorium, and there is still little sign of recovery in either total abundance or spatial spread of the total population (Anonymous 1998). However, there is some evidence of increased abundances in inshore areas (Anonymous 1998). In contrast, the metapopulation model predicts at least a limited recovery in the proportion of occupied areas after 10 years (Figures 4.3, 4.4). So why is there no sign of the predicted recovery?

One reason may be that the remaining subpopulations have not increased in abundance to the point where sufficient numbers of colonizing adults or larvae have been produced. The growth rates of individual subpopulations may be relatively low; Myers et al. (1997b) have estimated a maximum intrinsic rate of natural increase of $r_m = 0.17$ for

northern cod as a whole. This value of r_m was one of the lowest estimates in an analysis of 20 different cod stocks.

Alternatively, growth of the these subcomponents may be curtailed by losses due to incidental harvesting. Even though there is no directed commercial fishery for northern cod, a small but perhaps important amount of cod is still caught in the "sentinel" fishery and as bycatch in ongoing fisheries for other species. The Stock Status Report for northern cod published by the Department of Fisheries and Oceans states that approximately 15 000 tonnes of northern cod has been harvested from 1993 to 1997 (Anonymous 1998), with about 1000 tonnes caught per year since 1994. Fishing mortality on inshore subpopulations may still be high enough to have an influence on population growth. It should be noted, however, that the catch rates in the "sentinel fishery" have increased steadily in the last few years (Anonymous 1998). While the influence of fishing on recolonization of empty areas cannot be directly quantified, the effect may still exist ($e_F > 0$).

A third possibility for the absence of a detectable recovery may be the loss of individuals through increased natural mortality. For instance, much interest is currently centred on the possible impact upon northern cod of the increased abundance of a major predator, the harp seal, *Phoca groenlandica* (Gagné 1999).

The model predictions may be overly optimistic due to incorrect parameter estimates. Lower values for the colonization and extinction parameters will still result in relatively high proportions of occupied areas at equilibrium, as long as the ratio of these parameters remains the same as in the model simulations (i.e. m is much larger than e).

For instance, values of 0.3 yr^{-1} and 0.03 yr^{-1} for m and e respectively (as I estimated for northern cod in the absence of harvesting), result in an equilibrium P of 0.9 (Figure 4.3). Note that for a value of m 10 times the value of e, P will be 0.9; for example, values of m = 0.1 yr^{-1} and e = 0.01 yr^{-1} still return P = 0.9 at equilibrium. However, lesser colonization rates result in greater elapsed time until equilibrium occupancy is attained. For example, using the parameter values m = 0.3 yr^{-1} and e = 0.03 yr^{-1}, it takes approximately 27 years to reach equilibrium (Table 4.2, Figure 4.3), but if these values are reduced as above to m = 0.1 yr^{-1} and e = 0.01 yr^{-1}, a period of about 100 years is necessary to attain equilibrium occupancy.

A time scale of greater than 30 years for either collapse or recovery in the proportion of occupied areas may be unlikely, however. Collapses and recoveries during the history of the northern cod fishery tended to occur over 10-30 year periods (see Lear and Parsons 1993; Hutchings and Myers 1995). This time range is similar to historical collapse and recovery periods reported for other Atlantic cod fisheries in Greenland (e.g. Cushing 1982), Iceland (Jónsson 1994), and the Barents Sea (Øiestad 1994).

The genetic techniques used to provide evidence for metapopulation structure in northern cod (Chapters 1 to 3) do not suggest the same levels of exchange between subpopulations. If differences in microsatellite DNA allele frequencies exist at the subpopulation level (e.g. Ruzzante et al. 1997; Ruzzante et al. in press) then the exchange of reproductively successful individuals between subpopulations must be relatively low; otherwise such differentiation would not develop. The genetic evidence would therefore suggest that due to low exchange rates, the rate of colonization of unoccupied areas

would be concomitantly low. Conversely, evidence for metapopulation structure supplied by mark-recapture studies of adult cod (e.g. Lear 1984) and the drift of eggs and larvae (e.g. Helbig et al. 1992) suggest higher rates of migration and (or) dispersal. These types of studies therefore suggest that colonization rates would be relatively high. What is unknown in these studies is whether exchanged individuals interbreed successfully within their "adopted" subpopulation.

4.4.4 Weaknesses and strengths of the metapopulation model

The metapopulation model I have used is based on the model of Levins (1970) in which space is treated implicitly rather than realistically. The Levins (1970) model describes only the presence or absence of subpopulations in habitat patches. Each subpopulation is considered to be equally connected to each other, and thus their spatial locations are ignored in the model (Hanski 1994b). A spatially realistic metapopulation model incorporates all information concerning the number, size, exact location, and connectivity of habitat patches (Hanski 1994b; Hanski and Simberloff 1997). The purpose of such models is to arrive at specific quantitative predictions about the dynamics of real metapopulations (Hanski and Simberloff 1997).

While a realistic treatment of space in the metapopulation model of northern cod would constitute a preferable representation of metapopulation structure, an implicit approach was used because at present there is not enough information to construct a spatially realistic model. Perhaps most importantly, the actual number of past and present spawning areas occupied by northern cod is unknown. Large expanses of coastal Labrador have yet to be surveyed for the purposes of subpopulation structure

determination. Additional subpopulations may exist, likely relatively small in area and abundance, in the fjords and bays of central and northern Labrador.

Another problem is that it is not possible, based on available data, to determine accurately the proper boundaries around the designated spawning areas. This is one reason why I portrayed the spawning locations as fairly extensive geographically in order to maximize the probability that all spawning would occur within the boundary of the area (Figure 1.3). During periods of high total population abundance, these boundaries may likely become less definite, especially for offshore spawning areas. However, it is important to recall from Chapter 1 that microsatellite genetic analyses and mark-recapture data suggest the cohesion of the subpopulation units. Individuals return each year to the same spawning location (with some straying) to generate enough reproductive isolation to result in subpopulation genetic differentiation.

A potential weakness of the Levins (1970) model is that the internal population dynamics of subpopulations are essentially ignored; a patch (spawning area) is considered either empty or occupied, with no treatment of the demographics of subpopulations. This is a necessary simplification since few data exist concerning the internal dynamics of northern cod subpopulations. Separate census data for each putative subpopulation does not exist. Rather, abundance estimates exist only at the greater spatial scale of the entire metapopulation (northern cod stock complex), and only for a relatively short time series (approximately 20 years; Anonymous 1998). This lack of resolution at the subpopulation spatial scale currently prevents the determination of subpopulation-specific colonization and extinction rates.

It is therefore a necessary simplifying assumption that northern cod exists as a strict, Levins style metapopulation (see Chapter 1). For example, the subpopulation associated with the area of Hamilton Bank is orders of magnitude larger than the subpopulation located in Gilbert Bay (Figure 1.1). Due to the model's implicit nature, however, all spawning areas are treated as equivalent in extent and isolation. This is unavoidable as there is a lack of adequate data concerning the rates of exchange between spawning areas. While a mark-recapture database does exist for northern cod (Taggart et al. 1995), it does not have the spatial and temporal resolution required to generate accurate estimates of exchange rates of adults among all population subcomponents during the spawning season. In a spatially realistic metapopulation model, such information would be useful in the calculation of specific exchange rates between all possible pairs of subpopulations within the metapopulation. Parameterizing these linkages would provide insight to the possible existence of a rescue effect for some subpopulations, suggesting a relationship more akin to source-sink dynamics (Pulliam 1988) than a true "classical" metapopulation wherein all subpopulations are equal in size and degree of isolation.

4.4.5 Alternate spatial models of mobile marine fishes

Several models have been proposed to explain the observed patchy distributions (e.g. Steele 1977) of organisms in marine ecosystems. Marine fishes are no exception to this general rule of patchiness, and exhibit varying density on a range of temporal and spatial scales. Most mobile marine fish populations with large geographic ranges undergo increases in local density during the spawning season. In addition, populations of

temperate or near-arctic species such as cod usually have at least one defined spawning area (and period), which is occupied with some degree of interannual fidelity (e.g. Harden-Jones 1968; Cushing 1982).

The main question of interest has been: how do populations persist in particular geographic locations? An example of such an hypothesis is the "triangle of migration" proposed by Harden-Jones (1968). In this model, prespawning adult fish migrate against the prevailing current (contranatantly) to the spawning area and subsequently spawn. The adults then drift with the current (denatantly) away from the spawning area and return to the feeding grounds. Larvae drift from the spawning area to the nursery area, which is separate from the adult feeding ground.

In a later model fully developed by Sinclair (1988), the concept of spatial population persistence using the mechanisms of migration and drift was expanded into the "member\vagrant" hypothesis. This hypothesis states that the number of populations of a fish species is a function of the number and geographical location of areas within which the species can attain life cycle closure. The locations are oceanic gyres or other retention features that are geographically persistent from year to year. These systems, coupled with larval behaviour enhance local retention.

These early models describe the geographical persistence of entire populations, but do not address the phenomenon of intrapopulation differentiation in regional density exhibited by many fish species. An approach that does examine this characteristic is the "basin model" of MacCall (1990). MacCall used the concepts of density dependent habitat selection and the ideal free distribution to model the patchy distribution of

individuals within the range of a population. The crux of MacCall's model is that if the ideal free distribution functions within a fish population, then the spatial pattern of population density will correspond to basic habitat suitability.

The basin model is not at odds with the metapopulation concept. If areas of less suitable habitat exist within the population's range, these areas would be less densely occupied than surrounding area. With a decline in abundance, the population range would contract inward to areas of higher suitability. This contraction might be sufficient to cause the abandonment of less suitable areas in favour more suitable habitat. Under such conditions, the basin model would predict a spatial pattern resembling metapopulation structure. However, such a free-flow model does not explain the distinguishable genetic differences between subpopulations in northern cod.

4.4.6 Metapopulation structure in other demersal marine fishes

I contend that a number of demersal fish species with reproductive areas encompassed in large geographic ranges exhibit metapopulation structure during a segment of the seasonal reproductive cycle. During the spawning season most groundfish show intra-annual variance in regional density. The highest density variance is shown during the prespawning and spawning seasons, followed by a postspawning feeding dispersal. Local subpopulations often exhibit strong interannual fidelity to specific geographical spawning areas.

This spatial segregation during the spawning season is displayed by the cod (*Gadus morhua*) stocks off Norway, where coastal (fjord) cod are considered to be genetically and behaviourally distinct from migratory Northeast Arctic cod (Jakobsen 1987; Dahle

1991; Salvanes and Ulltang 1992; Dahle and Jørstad 1993). Northeast Arctic cod spawn in several areas along the nearshore banks. Spawning occurs mainly at Lofoten, but also to the north near Sørøy and to the south as far as Møre (Bergstad et al. 1987). Evidence from tagging experiments indicates that spawners return to their location of first spawning in subsequent spawning seasons (Gødø 1984). Coastal cod, found in the fjords and nearshore areas of Norway, are considered a subpopulation separate from Northeast Arctic cod (Gødø and Moksness 1987). The spawning subpopulations in the coastal areas are often comprised of two elements. One unit is resident in the area year-round, and the other unit includes individuals that migrate from neighbouring fjords and offshore areas (Gødø 1984; Jakobsen 1987; Salvanes and Ulltang 1992), yet these subpopulations remain genetically distinct. Regardless of the question of distinct populations, it is important to note that both inshore (Jakobsen 1987) and offshore (Bergstad et al. 1987) spawning occurs in predictable areas year after year.

Some other fish populations may be structured as metapopulations. Barents Sea saithe (*Polliachius virens*) is another abundant, commercially exploited population that exhibits discrete spawning areas within its overall range. Saithe spawn on the coastal banks off Møre, Haltenbanken and Lofoten, and in the northern North Sea (Bergstad et al. 1987). This stock has shown fairly substantial emigration to stocks found around Iceland and the Faroe Islands (Jakobsen and Olsen 1987).

Recently, other researchers have advocated the utilization of a metapopulation approach in describing the spatial dynamics of marine fishes. Bailey (1998) and Bailey et al. (in press) have proposed the existence of generalized metapopulation structure in

walleye pollock, *Theragra chalcogramma*. McQuinn (1997) has suggested that the structure and dynamics of Atlantic herring (*Clupea harengus*) may best be described within the metapopulation concept. To date, however, no modelling analyses of metapopulation dynamics have been undertaken for marine fishes with large geographic ranges.

4.4.7 Generalizing the metapopulation approach for demersal marine fishes

Investigations of the spatial dynamics of commercially important groundfish stocks are usually performed using data from annual research trawling surveys. Such surveys are undertaken during the same period every year, and usually have a limited duration. For instance the research survey for northern cod is carried out over a 8-10 week period from October through December (e.g. Shelton et al. 1996). However, there is variation in the timing of large scale movements and migrations of fish stocks. Most large populations undergo seasonal feeding-spawning migrations (e.g. Harden-Jones 1968) that may be adaptations for high abundances (Nikolsky 1963). The timing of these migrations varies interannually in response to environmental stimuli such as temperature that also vary around a mean seasonal cycle (Smith 1985; see Colbourne et al. 1997 for northern cod). Such interannual variation in the seasonal distribution of populations may temporally alias the results of studies that calculate fish distributions from assessment survey data (e.g. Swain and Wade 1993; Marshall and Frank 1994; Marshall and Frank 1995). This complication is in addition to problems inherent in most distributional indices derived from survey data (see Marshall and Frank 1994).

Levins' (1970) metapopulation model estimates the proportion of suitable areas that are occupied, rather than the number of individuals in each area. Thus, local dynamics such as growth and predation are ignored in simpler forms of the model. This is useful because mark-recapture studies often lack the spatial resolution necessary to "map" intrahabitat abundance or density. With a metapopulation approach, one is interested only in how discrete subcomponents interact to form a dynamic metapopulation spread across a large range.

Table 4.1. Some factors influencing the metapopulation dynamics of northern cod, where *m* is the colonization parameter and *e* is the extinction parameter.

Influence *m*	Influence *e*
population growth rate (*r*)	natural mortality rate
lifespan	lifespan
mobility	weather
currents	climate
migration	currents
shoaling behaviour	prey distributions
interoparity	predator abundance
"generalist" species (very adaptable)	disease
	fishing

Table 4.2. Length of time required to reach equilibrium proportion of occupied areas under a range of initial occupancy rates. The colonization parameter is held constant at $m = 0.3$ yr^{-1}, and the extinction parameter is increased by multiples of $e = 0.03$ yr^{-1}. The equilibrium proportion of occupied areas (P_E) is listed below the extinction parameter value.

	Length of time required to reach equilibrium proportion of occupied areas (years)				
Initial proportion of occupied areas (P)	**$e = 0.03$ ($P_E = 0.9$)**	**$e = 0.06$ ($P_E = 0.8$)**	**$e = 0.09$ ($P_E = 0.7$)**	**$e = 0.12$ ($P_E = 0.6$)**	**$e = 0.15$ ($P_E = 0.5$)**
0.1	27	29.5	32.5	35.5	40
0.2	24	26	28	30.5	33.5
0.3	22	23.5	25	27	28
0.4	20.5	21.5	22.5	23	21.5
0.5	18.5	19	19.5	18	0
0.6	17	17	15	0	19
0.7	15	13.5	0	15.5	22.5
0.8	12	0	14	19	24.5
0.9	0	12.5	16.5	21	25.5
0.95	8.5	13.5	17.5	21.5	26

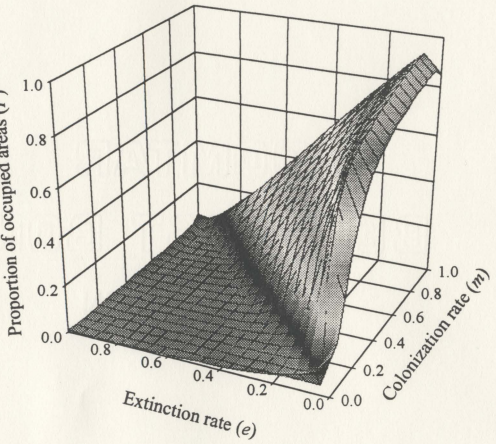

Figure 4.1. Three-dimensional representation of the equilibrium (steady state) solutions for the Levins (1970) metapopulation model, showing the change in proportion of occupied spawning areas (P) under a range of colonization (m) and extinction (e) parameter values.

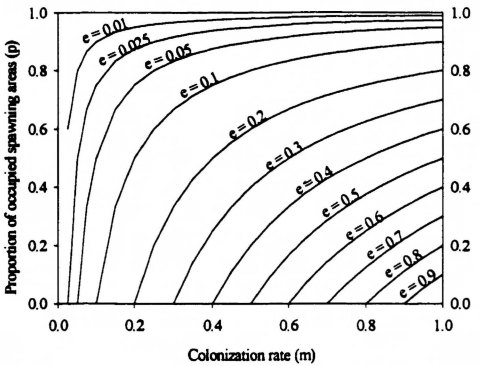

Figure 4.2. Two-dimensional representation of the equilibrium (steady state) solutions for the Levins (1970) metapopulation model, showing the change in proportion of occupied spawning areas (P) under a range of colonization (m) and extinction (e) parameter values.

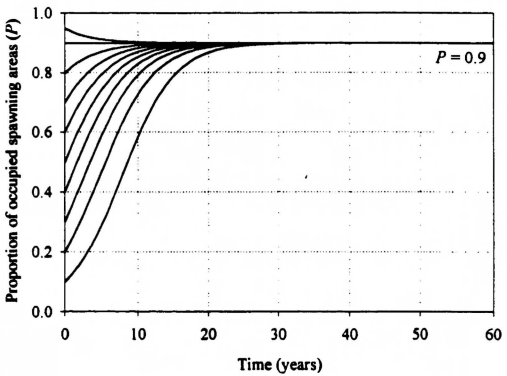

Figure 4.3.1. Dynamics of the metapopulation model with an extinction parameter value of $e = 0.03$ yr^{-1} and a colonization parameter value of $m = 0.3$ yr^{-1}, under a range of initial proportions of occupied spawning areas.

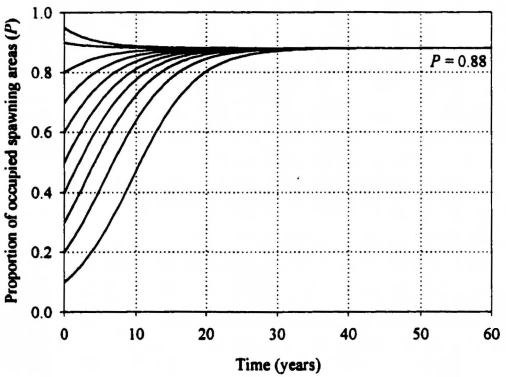

Figure 4.3.2. Dynamics of the metapopulation model with an extinction parameter value of $e = 0.03$ yr^{-1} and a colonization parameter value of $m = 0.25$ yr^{-1}, under a range of initial proportions of occupied spawning areas.

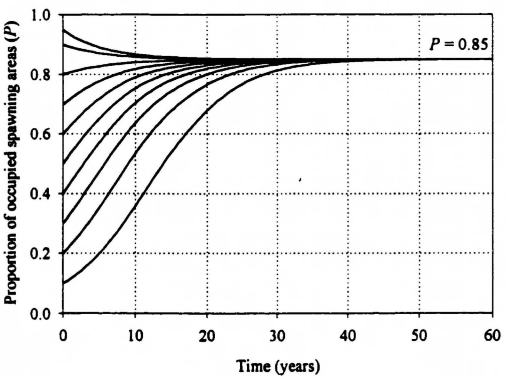

Figure 4.3.3. Dynamics of the metapopulation model with an extinction parameter value of $e = 0.03$ yr^{-1} and a colonization parameter value of $m = 0.2$ yr^{-1}, under a range of initial proportions of occupied spawning areas.

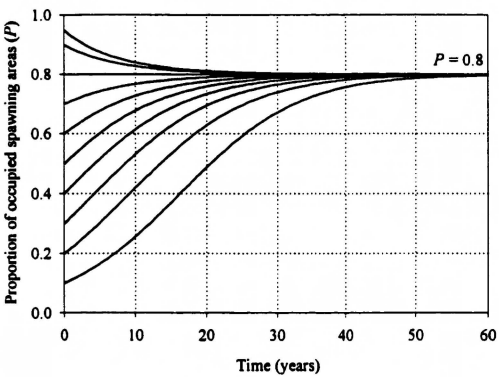

Figure 4.3.4. Dynamics of the metapopulation model with an extinction parameter value of $e = 0.03$ yr^{-1} and a colonization parameter value of $m = 0.15$ yr^{-1}, under a range of initial proportions of occupied spawning areas.

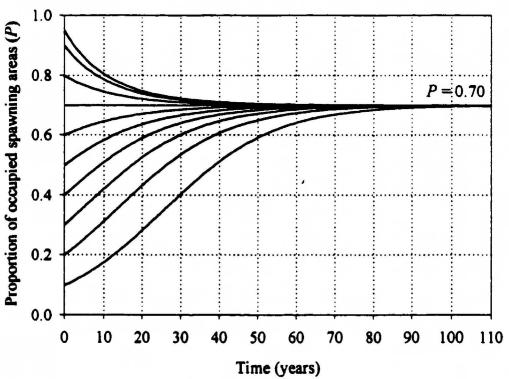

Figure 4.3.5. Dynamics of the metapopulation model with an extinction parameter value of $e = 0.03$ yr^{-1} and a colonization parameter value of $m = 0.1$ yr^{-1}, under a range of initial proportions of occupied spawning areas.

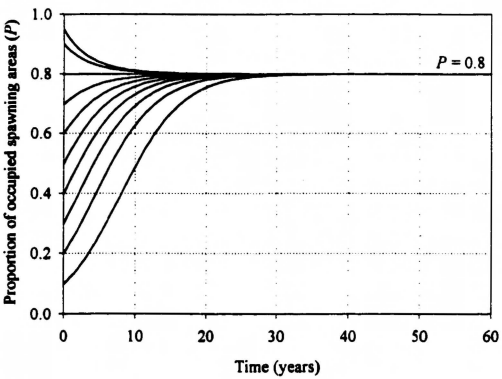

Figure 4.4.1. Dynamics of the metapopulation model with a colonization parameter value of $m = 0.3$ yr^{-1} and an extinction parameter value of $e = 0.06$, under a range of initial proportions of occupied spawning areas.

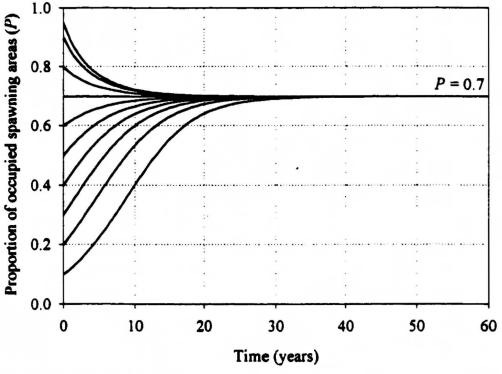

Figure 4.4.2. Dynamics of the metapopulation model with a colonization parameter value of $m = 0.3$ yr^{-1} and an extinction parameter value of $e = 0.09$, under a range of initial proportions of occupied spawning areas.

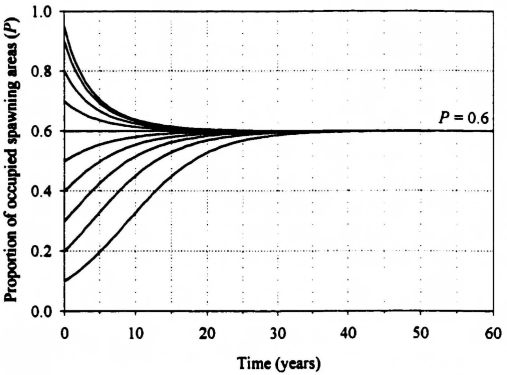

Figure 4.4.3. Dynamics of the metapopulation model with a colonization parameter value of $m = 0.3$ yr^{-1} and an extinction parameter value of $e = 0.12$, under a range of initial proportions of occupied spawning areas.

Chapter 5: Summary and conclusions

5.1 Summary

In this dissertation I have proposed that northern cod may be considered a metapopulation, a set of local populations within some larger area where typically migration from one local population to at least some other subpopulation is possible (Hanskii and Simberloff 1997). Evidence for the semi-isolation of offshore spawning components is derived from a number of sources. Metapopulation subdivision is supported by the observed temporal stability of occupancy of specific spawning areas. The fidelity of spawning sites is suggested by mark-recapture studies, and is indirectly supported by the sampling of adult cod in spawning condition, and in egg and larval surveys. The existence of subpopulation structure is further upheld by analyses of life-history and morphometric characteristics, and more recently with large scale genetic studies.

Reports of inshore overwintering and spawning have indicated the possibility of inshore subcomponents of northern cod. With collaborators, I undertook two separate studies to ascertain the existence of inshore subpopulations. The existence of a local subpopulation in Trinity Bay, Newfoundland, is supported by data from original and published studies of (*i*) spawning times and locations within the bay, (*ii*) mark-recapture analysis of adult cod, and (*iii*) differentiation of microsatellite allele frequencies in northern cod. Spawning periods were consistent interannually, ranging from late spring to late

summer. Mark-recapture and sonic tracking studies demonstrated that cod are resident in Trinity Bay year round, and that most cod marked in the spring remain in the area for at least several years. Analysis of microsatellite allele frequencies revealed that cod overwintering in Trinity Bay are genetically distinct from some other components of northern cod. From these observations I concluded that a subpopulation is present in Trinity Bay.

In continued collaboration with others (Ruzzante et al. in press), I selected the area of Gilbert Bay, Labrador, as a second possible location of a coastal subpopulation. Cod sampled in Gilbert Bay were significantly smaller in length-, weight- , and fecundity-at-age than cod from similar latitudes offshore and from cod in Trinity Bay. These fish are also genetically distinct from the rest of northern cod. Thus, cod from Gilbert Bay grow more slowly, are less fecund, and are at least semi-isolated reproductively from other components of northern cod. Gilbert Bay cod, therefore, also constitute a local subpopulation of northern cod.

Following these field studies, I constructed a conceptual model of the metapopulation dynamics of northern cod. I modified the original model of Levins (1970) to include implicitly the effects of harvesting on the spatial dynamics of northern cod. I derived first approximations of the values for model colonization and extinction parameters. The model predicts the extinction of some subpopulations under continual and intensive fishing effort. The time period necessary for a recovery, and the spatial extent of this recovery (as measured by the reoccupation of empty spawning areas) is also influenced by the intensity of harvest. In presenting this model I propose that

recolonization is achieved by aggregations of mature cod and drifting larvae that successfully reproduce in the newly colonized spawning area in subsequent years.

5.2 Recommendations for future research

I believe that the next phase of modelling analysis of northern cod is to move from implicit to realistic approaches in representing the metapopulation dynamics of this population. In order to construct these more realistic models, additional information is required. The subcomponents of northern cod are unequal in geographic extent and obviously differ in abundance as well. These characteristics have implications in metapopulation dynamics. For example, a large subpopulation is less likely to become extinct than a relatively smaller (less abundant) subpopulation. Therefore, the extinction rates for individual subpopulations would vary. The specification of these individual rates requires knowledge of each subpopulation. Acquiring this information requires that studies be undertaken on each population subcomponent; a finer spatial scale resolution than current stock assessment surveys. For monitoring the recovery, surveys would have to be extended to coastal areas to assess inshore subpopulations and their spawning areas, which is very difficult in light of the lack of trawlable bottom in the inshore and the need to maintain standardized sampling protocols. The feasibility of additional assessment surveys is questionable, given the extra cost and the current low monetary value of the northern cod fishery. As an interim measure, if spawning areas are recolonized in the future, differences in subpopulation-specific extinction rates could modelled on an ordinal or rank scale, from lowest to highest probability of extinction. While this approach may

not require assessment surveys for each subpopulation, an accurate, relative ranking requires more information than is currently available.

Reasonably accurate estimates of the rate of exchange of individuals among the constituent subpopulations of the northern cod metapopulation also is required for a spatially realistic metapopulation model. The exchange of individuals can have an important effect on metapopulation dynamics through the "rescue effect", thus decreasing a subpopulation's probability of extinction. These rates also provide insight into the relative isolation of individual subpopulations. For example, spatially distant subpopulations may exchange fewer strays than subpopulations occupying neighbouring spawning areas, and exhibit less synchrony in their dynamics.

Necessary data concerning the exchange of adults might be obtained through a synoptic mark-recapture program. Tagging could be undertaken upon each subpopulation during the spawning season, to maximize the probability of assigning spawners as members of their true subpopulation. Only recaptures from designated spawning periods would be used in analyses of metapopulation dynamics. Tagging could be repeated annually to determine if exchange rates, and therefore model parameters vary with time.

Assessment of the relative importance of larval drift is more problematic. Mapping egg and larval drift patterns is not sufficient. The origin of successful colonizers would have to be ascertained (e.g. Heath 1989; Ruzzante et al. 1996).

Assisted by these new data, more sophisticated metapopulation models may aid in addressing questions concerning the recovery of northern cod. Metapopulation structure should be taken into account in the management strategy of a future commercial fishery.

Spawning aggregations (subpopulations) are targeted easily in a commercial fishery due to the seasonal predictability of their location. Shoal densities can remain high under sustained exploitation, even as subpopulation abundance declines to very low levels (Hutchings 1996). This "escalation of catchability" (Beverton 1990) can result in the rapid commercial extinction of specific population components. The existence of subpopulation genetic differentiation leads to issues of the conservation of genetic diversity in this metapopulation under a directed fishery (Ruzzante et al. in press). Regardless of genetic subdivision, metapopulation structure has potentially important implications for successful fishery management (Smedbol 1998). The potential loss of specific subpopulations would entail a concomitant loss of phenotypic characteristics, including behavioural adaptations to local conditions as expressed during life history, e.g. migration routes, and the timing and location of spawning (Rose 1993).

Populations of many marine fish species undergo periods of mixing (and isolation) that are usually related to feeding (and reproduction). The metapopulation approach may be an umbrella concept under which to unite the various patterns, behaviours, and strategies identified by researchers as influential in the spatial dynamics of marine fish species.

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Appendix A. Data from northern Atlantic cod (*Gadus morhua*) sampled in Gilbert Bay, Labrador during August 1996 (n = 122).

Fish # or Tag #	Length (cm)	Age (years)	Whole weight (kg)	Fish # or Tag #	Length (cm)	Age (years)	Whole weight (kg)
1	50.0	9	1.25	30	50.5	9	---
2	69.5	10	3.12	31	43.5	5	---
3	47.0	7	1.15	32	51.0	9	---
4	46.0	5	1.01	33	43.5	5	---
5	43.0	4	1.10	34	39.5	5	---
6	51.5	8	1.39	35	44.0	5	---
7	44.0	10	0.81	36	42.5	5	---
8	41.0	6	0.73	37	49.5	6	---
9	41.0	9	0.68	38	47.5	7	---
10	38.5	4	0.57	39	52.5	5	---
11	42.0	5	0.73	40	66.0	6	---
12	63.5	5	2.53	41	42.5	5	---
13	40.0	9	0.62	42	46.5	5	---
14	46.0	8	1.01	43	42.5	5	---
15	46.5	5	0.85	44	41.0	8	---
16	51.5	10	1.35	45	38.5	8	---
17	41.0	6	0.75	46	44.5	7	---
18	42.0	4	0.81	47	44.5	8	---
19	51.0	7	1.24	48	45.5	5	---
20	49.5	5	1.09	49	43.0	8	---
21	63.5	9	3.64	50	42.0	5	---
22	42.0	4	1.36	51	51.0	5	---
23	47.5	6	1.82	52	51.5	8	---
24	41.0	5	1.36	53	44.0	6	---
25	53.0	11	---	54	42.0	8	---
26	45.0	9	---	55	43.0	6	---
27	51.5	5	---	56	48.0	6	---
28	51.0	9	---	57	49.5	8	---
29	58.0	7	---	58	56.5	9	---

Fish # or Tag #	Length (cm)	Age (years)	Whole weight (kg)
59	53.0	6	---
60	54.0	9	---
61	44.0	9	---
62	48.0	6	---
63	43.5	5	---
64	42.5	6	---
65	44.5	6	---
66	41.0	6	---
67	44.5	6	---
68	48.5	9	---
69	49.5	6	---
70	49.0	9	---
71	50.0	9	---
746	43.0	6	---
916	50.0	9	---
887	46.0	10	---
888	43.0	7	---
802	66.0	10	---
755	42.0	6	---
844	46.5	6	---
850	54.0	9	---
889	41.5	6	---
870	44.0	6	---
752	42.0	10	---
769	42.0	5	---
900	49.5	10	---
816	45.0	6	---
766	42.0	6	---
913	42.5	9	---
827	47.0	7	---
837	51.0	9	---
771	53.5	5	---
925	54.5	11	---
817	56.5	10	---
767	47.0	6	---
907	47.5	6	---
873	44.0	6	---
778	52.0	5	---
859	67.5	11	---
824	44.0	8	---
833	55.5	11	---
648	41.5	5	---
668	45.5	6	---
921	48.0	6	---
760	47.5	8	---
820	43.0	8	---
691	43.5	9	---
823	46.0	6	---
860	46.5	8	---
811	43.0	6	---
628	47.5	6	---
781	45.5	7	---
885	43.0	6	---
839	48.0	6	---
893	47.0	5	---
834	47.0	9	---
843	47.5	7	---
647	50.0	9	---
886	41.5	6	---
869	48.5	8	---
902	52.5	8	---
812	46.5	7	---
842	51.0	8	---
818	48.0	6	---

Appendix B. Length and weight of northern Atlantic cod (*Gadus morhua*) sampled in Gilbert Bay, Labrador, during October 1996.

Fish #	Length (cm)	Whole weight (kg)
1	44.5	0.80
2	49.0	1.10
3	46.0	1.00
4	50.5	1.30
5	52.5	1.75
6	58.0	2.10
7	63.0	2.50
8	65.0	2.60
9	52.0	1.50
10	52.0	1.40
11	54.0	1.60
12	56.0	1.80

Appendix C. Data from northern Atlantic cod (*Gadus morhua*) sampled in Gilbert Bay, Labrador on May 27, 1997.

Fish #	Length (cm)	Wet weight (kg)	Age (years)	Sex	Maturity	Gonad weight (kg)	Liver weight (kg)	Gutted weight (kg)	Condition factor	Potential fecundity (oocytes)	Relative fecundity (oocytes·g^{-1})
1	39.0	0.53	5	F	MAT.BP	0.06	0.02	0.41	0.893	309552	658.62
2	45.0	0.84	6	F	MAT.P	0.06	0.01	0.73	0.922	255858	328.02
3	47.0	0.96	10	F	MAT.P	0.10	0.04	0.79	0.925	434755	505.53
4	50.5	1.21	7	M	MAT.P	0.11	0.05	1.00	0.940		
5	41.0	0.55	5	M	IMM	0.01	0.01	0.50	0.798		
6	51.0	1.12	6	M	MAT.P	0.11	0.04	0.96	0.844		
7	38.5	0.55	5	F	MAT.AP	0.06	0.02	0.44	0.964	203837	415.1
8	45.5	0.84	6	F	MAT.P	0.15	0.04	0.62	0.892	334879	485.33
9	42.5	0.68	4	M	MAT.P	0.05	0.01	0.59	0.886		
10	49.0	0.93	7	F	MAT.P	0.09	0.03	0.78	0.790	478328	569.44
11	57.5	1.58	6	F	MAT.BP	0.20	0.05	1.22	0.831	360832	261.47
12	52.5	1.43	5	M	MAT.P	0.10	0.05	1.23	0.988		
13	39.5	0.52	6	M	MAT.P	0.05	0.01	0.42	0.844		
14	44.5	0.68	6	M	MAT.P	0.04	0.01	0.62	0.772		
15	39.0	0.55	5	M	MAT.P	0.04	0.02	0.48	0.927		
16	51.0	1.26	9	F	MAT.P	0.19	0.03	0.92	0.950	177647	166.03
17	45.0	0.84	8	M	MAT.P	0.05	0.02	0.71	0.922		
18	47.5	1.06	7	M	MAT.P	0.05	0.04	0.92	0.989		

Fish #	Length (cm)	Wet weight (kg)	Age (years)	Sex	Maturity	Gonad weight (kg)	Liver weight (kg)	Gutted weight (kg)	Condition factor	Potential fecundity (oocytes)	Relative fecundity (oocytes·g^{-1})
19	46.0	0.93	8	F	MAT.CP	0.20	0.03	0.60	0.955	217968	298.59
20	52.5	1.2	15	M	MAT.P	0.10	0.02	1.03	0.829		
21	50.5	1.15	6	M	MAT.P	0.08	0.02	1.01	0.893		
22	44.0	0.75	6	F	MAT.CP	0.14	0.01	0.57	0.880		
23	53.4	1.46	7	F	MAT.BP	0.20	0.05	1.14	0.959	350328	278.04
24	51.5	1.17	7	F	MAT.P	0.11	0.03	0.94	0.857	283756	267.69
25	50.0	1.02	6	F	spent L	0.01	0.05	0.92	0.816		
26	39.0	0.49	4	M	MAT.P	0.02	0.01	0.43	0.826		
27	49.0	1.03	6	F	MAT.P	0.11	0.04	0.83	0.875	551489	599.44
28	60.0	1.99	9	M	MAT.P	0.21	0.06	1.64	0.921		
29	52.5	1.27	8	M	MAT.P	0.07	0.02	1.11	0.878		
30	46.0	0.98	6	F	MAT.P	0.10	0.05	0.76	1.007	479220	544.57
31	40.0	0.54	6	F	IMM		0.01	0.47	0.844		
32	38.0	0.52	5	F	MAT.P	0.05	0.02	0.43	0.948	271897	578.5
33	48.5	1.1	6	M	MAT.P	0.07	0.03	0.95	0.964		
34	48.5	1.07	8	M	MAT.P	0.04	0.02	0.90	0.938		
35	48.5	1.05	5	M	MAT.P	0.05	0.04	0.89	0.920		
36	46.0	0.86	6	F	MAT.AP	0.08	0.03	0.71	0.884	287826	369.01
37	41.5	0.64		M	MAT.P	0.05	0.04	0.56	0.895		

Appendix D. Data from northern Atlantic cod (*Gadus morhua*) sampled in Gilbert Bay, Labrador during 1996 and 1997 (n = 159), in Trinity Bay, April, 1995 (n = 50), and during the Department of Fisheries and Oceans research vessel (RV) survey in North Atlantic Fisheries Organization (NAFO) Division 2J, 1978-1995 (see Tables 31a and 32b in Shelton et al. 1996). The 2J RV data are means-at-age.

Gilbert Bay			Trinity Bay			2J RV survey			
Age (years)	Length (cm)	Whole weight (kg)	Age (years)	Length (cm)	Whole weight (kg)	Survey year	Age (years)	Length (cm)	Whole weight (kg)
9	50.0	1.25	5	46	0.785	1978	2	29	0.223
10	69.5	3.12	5	49	0.960	1978	3	38	0.487
7	47.0	1.15	5	51	1.070	1978	4	46	0.947
5	46.0	1.01	5	52	1.060	1978	5	54	1.580
4	43.0	1.10	5	52	1.100	1978	6	60	2.199
8	51.5	1.39	5	52	1.215	1978	7	66	2.515
10	44.0	0.81	5	52	1.260	1978	8	69	3.862
6	41.0	0.73	5	52	1.325	1978	9	79	4.365
9	41.0	0.68	5	52	1.330	1978	10	80	5.771
4	38.5	0.57	5	53	1.140	1978	11	87	6.358
5	42.0	0.73	5	53	1.170	1978	12	90	9.736
5	63.5	2.53	5	53	1.205	1979	2	30	0.263
9	40.0	0.62	5	53	1.240	1979	3	41	0.682
8	46.0	1.01	5	53	1.395	1979	4	48	1.023
5	46.5	0.85	5	53	1.465	1979	5	56	1.593
10	51.5	1.35	5	54	1.260	1979	6	61	2.379
6	41.0	0.75	5	54	1.325	1979	7	68	2.748
4	42.0	0.81	5	54	1.435	1979	8	74	2.753
7	51.0	1.24	5	56	1.445	1979	9	69	6.193
5	49.5	1.09	5	56	1.575	1979	10	77	5.428
9	63.5	3.64	5	57	1.780	1979	11	87	7.191
4	42.0	1.36	5	57	1.815	1979	12	86	6.206
6	47.5	1.82	5	57	1.985	1980	2	31	0.240

Gilbert Bay			Trinity Bay			2J RV survey			
Age (years)	Length (cm)	Whole weight (kg)	Age (years)	Length (cm)	Whole weight (kg)	Survey year	Age (years)	Length (cm)	Whole weight (kg)
5	41.0	1.36	5	59	1.830	1980	3	39	0.528
5	39.0	0.53	5	51	1.110	1980	4	50	1.046
6	45.0	0.84	6	52	1.255	1980	5	54	1.363
10	47.0	0.96	6	53	1.230	1980	6	61	2.055
7	50.5	1.21	6	57	1.400	1980	7	64	2.548
5	41.0	0.55	6	57	1.670	1980	8	70	3.090
6	51.0	1.12	6	58	1.540	1980	9	82	5.986
5	38.5	1.55	6	58	1.640	1980	10	83	7.628
6	45.5	1.84	6	59	1.590	1980	11	86	6.546
4	42.5	0.68	6	60	1.580	1980	12	87	7.723
7	49.0	0.93	6	60	1.660	1981	2	30	0.228
6	57.5	1.58	6	60	1.925	1981	3	39	0.548
5	52.5	1.43	6	62	2.130	1981	4	47	1.077
6	39.5	0.52	6	62	2.235	1981	5	55	1.663
6	44.5	0.68	6	63	2.375	1981	6	58	1.982
5	39.0	0.55	6	64	2.200	1981	7	63	2.519
9	51.0	1.26	6	67	2.185	1981	8	67	3.197
8	45.0	0.84	7	55	1.350	1981	9	73	3.944
7	47.5	1.06	7	58	1.590	1981	10	84	6.586
8	46.0	0.93	7	62	1.970	1981	11	90	6.906
15	52.5	1.20	7	62	2.455	1981	12	89	10.797
6	50.5	1.15	7	66	2.170	1982	2	30	0.215
6	44.0	0.75	8	63	2.495	1982	3	38	0.501
7	53.5	1.46	8	65	2.120	1982	4	47	0.955
7	51.5	1.17	8	70	2.600	1982	5	53	1.601
6	50.0	1.02	8	74	3.040	1982	6	59	2.004
4	39.0	0.49	9	85	5.730	1982	7	61	2.392
6	49.0	1.03	—	—	—	1982	8	64	2.686
9	60.0	1.99	—	—	—	1982	9	69	3.872
8	52.5	1.27	—	—	—	1982	10	77	6.507
6	46.0	0.98	—	—	—	1982	11	86	7.660

Gilbert Bay			Trinity Bay			2J RV survey			
Age (years)	Length (cm)	Whole weight (kg)	Age (years)	Length (cm)	Whole weight (kg)	Survey year	Age (years)	Length (cm)	Whole weight (kg)
6	40.0	0.54	---	---	---	1982	12	95	10.055
5	38.0	0.52	---	---	---	1983	2	26	0.176
6	48.5	1.10	---	---	---	1983	3	39	0.587
8	48.5	1.07	---	---	---	1983	4	46	0.956
5	48.5	1.05	---	---	---	1983	5	54	1.554
6	46.0	0.86	---	---	---	1983	6	60	1.853
11	53.0	---	---	---	---	1983	7	63	2.252
9	45.0	---	---	---	---	1983	8	65	2.773
5	51.5	---	---	---	---	1983	9	69	3.346
9	51.0	---	---	---	---	1983	10	74	4.022
7	58.0	---	---	---	---	1983	11	75	4.165
9	50.5	---	---	---	---	1983	12	95	8.946
5	43.5	---	---	---	---	1984	2	27	0.153
9	51.0	---	---	---	---	1984	3	34	0.384
5	43.5	---	---	---	---	1984	4	44	0.829
5	39.5	---	---	---	---	1984	5	51	1.303
5	44.0	---	---	---	---	1984	6	57	1.782
5	42.5	---	---	---	---	1984	7	63	2.388
6	49.5	---	---	---	---	1984	8	66	2.562
7	47.5	---	---	---	---	1984	9	67	3.023
5	52.5	---	---	---	---	1984	10	72	3.459
6	66.0	---	---	---	---	1984	11	78	5.669
5	42.5	---	---	---	---	1984	12	83	6.539
5	46.5	---	---	---	---	1985	2	27	0.200
5	42.5	---	---	---	---	1985	3	34	0.363
8	41.0	---	---	---	---	1985	4	40	0.622
8	38.5	---	---	---	---	1985	5	49	0.138
7	44.5	---	---	---	---	1985	6	53	1.486
8	44.5	---	---	---	---	1985	7	58	1.880
5	45.5	---	---	---	---	1985	8	64	2.497
8	43.0	---	---	---	---	1985	9	67	2.652

Gilbert Bay			Trinity Bay			2J RV survey			
Age (years)	Length (cm)	Whole weight (kg)	Age (years)	Length (cm)	Whole weight (kg)	Survey year	Age (years)	Length (cm)	Whole weight (kg)
5	42.0	—	—	—	—	1985	10	70	3.223
5	51.0	—	—	—	—	1985	11	73	4.178
8	51.5	—	—	—	—	1985	12	76	4.014
6	44.0	—	—	—	—	1986	2	28	0.254
8	42.0	—	—	—	—	1986	3	36	0.350
6	43.0	—	—	—	—	1986	4	41	0.645
6	48.0	—	—	—	—	1986	5	48	1.054
8	49.5	—	—	—	—	1986	6	53	1.660
9	56.5	—	—	—	—	1986	7	57	1.914
6	53.0	—	—	—	—	1986	8	60	2.292
9	54.0	—	—	—	—	1986	9	68	3.810
9	44.0	—	—	—	—	1986	10	68	4.513
6	48.0	—	—	—	—	1986	11	72	4.638
5	43.5	—	—	—	—	1986	12	77	6.161
6	42.5	—	—	—	—	1987	2	29	0.266
6	44.5	—	—	—	—	1987	3	36	0.545
6	41.0	—	—	—	—	1987	4	43	0.913
6	44.5	—	—	—	—	1987	5	49	1.355
9	48.5	—	—	—	—	1987	6	52	1.483
6	49.5	—	—	—	—	1987	7	57	2.067
9	49.0	—	—	—	—	1987	8	59	2.409
9	50.0	—	—	—	—	1987	9	61	1.818
6	43.0	—	—	—	—	1987	10	68	4.648
9	50.0	—	—	—	—	1987	11	77	4.550
10	46.0	—	—	—	—	1987	12	75	4.649
7	43.0	—	—	—	—	1988	2	31	0.253
10	66.0	—	—	—	—	1988	3	37	0.553
6	42.0	—	—	—	—	1988	4	44	0.819
6	46.5	—	—	—	—	1988	5	48	1.145
9	54.0	—	—	—	—	1988	6	53	1.653
6	41.5	—	—	—	—	1988	7	56	1.690

Gilbert Bay			Trinity Bay			2J RV survey			
Age (years)	Length (cm)	Whole weight (kg)	Age (years)	Length (cm)	Whole weight (kg)	Survey year	Age (years)	Length (cm)	Whole weight (kg)
6	44.0	—	—	—	—	1988	8	60	2.379
10	42.0	—	—	—	—	1988	9	63	2.717
5	42.0	—	—	—	—	1988	10	66	2.880
10	49.5	—	—	—	—	1988	11	74	3.868
6	45.0	—	—	—	—	1988	12	80	6.732
6	42.0	—	—	—	—	1989	2	28	0.204
9	42.5	—	—	—	—	1989	3	38	0.488
7	47.0	—	—	—	—	1989	4	44	0.810
9	51.0	—	—	—	—	1989	5	50	1.263
5	53.5	—	—	—	—	1989	6	54	1.567
11	54.5	—	—	—	—	1989	7	57	1.907
10	56.5	—	—	—	—	1989	8	59	2.259
6	47.0	—	—	—	—	1989	9	61	2.616
6	47.5	—	—	—	—	1989	10	61	3.143
6	44.0	—	—	—	—	1989	11	69	3.771
5	52.0	—	—	—	—	1989	12	67	3.206
11	67.5	—	—	—	—	1990	2	27	0.158
8	44.0	—	—	—	—	1990	3	35	0.355
11	55.5	—	—	—	—	1990	4	42	0.697
5	41.5	—	—	—	—	1990	5	47	0.987
6	45.5	—	—	—	—	1990	6	53	1.462
6	48.0	—	—	—	—	1990	7	56	1.784
8	47.5	—	—	—	—	1990	8	59	2.108
8	43.0	—	—	—	—	1990	9	61	2.299
9	43.5	—	—	—	—	1990	10	61	2.539
6	46.0	—	—	—	—	1990	11	71	4.397
8	46.5	—	—	—	—	1990	12	70	4.340
6	43.0	—	—	—	—	1991	2	28	0.187
6	47.5	—	—	—	—	1991	3	34	0.307
7	45.5	—	—	—	—	1991	4	39	0.581
6	43.0	—	—	—	—	1991	5	44	0.743

Gilbert Bay			Trinity Bay			2J RV survey			
Age (years)	Length (cm)	Whole weight (kg)	Age (years)	Length (cm)	Whole weight (kg)	Survey year	Age (years)	Length (cm)	Whole weight (kg)
6	48.0	---	---	---	---	1991	6	52	1.139
5	47.0	---	---	---	---	1991	7	57	1.540
9	47.0	---	---	---	---	1991	8	59	1.692
7	47.5	---	---	---	---	1991	9	63	2.367
9	50.0	---	---	---	---	1991	10	65	2.721
6	41.5	---	---	---	---	1991	11	74	3.963
8	48.5	---	---	---	---	1991	12	65	3.391
8	52.5	---	---	---	---	1992	2	26	0.139
7	46.5	---	---	---	---	1992	3	34	0.318
8	51.0	---	---	---	---	1992	4	39	0.482
6	48.0	---	---	---	---	1992	5	42	1.620
---	---	---	---	---	---	1992	6	46	1.844
---	---	---	---	---	---	1992	7	60	1.478
---	---	---	---	---	---	1993	2	26	0.153
---	---	---	---	---	---	1993	3	62	0.300
---	---	---	---	---	---	1993	4	41	0.575
---	---	---	---	---	---	1993	5	44	0.751
---	---	---	---	---	---	1993	6	48	0.923
---	---	---	---	---	---	1993	7	46	0.860
---	---	---	---	---	---	1994	2	26	0.155
---	---	---	---	---	---	1994	3	36	0.433
---	---	---	---	---	---	1994	4	42	0.646
---	---	---	---	---	---	1994	5	47	0.909
---	---	---	---	---	---	1994	6	56	1.664
---	---	---	---	---	---	1994	7	56	1.700
---	---	---	---	---	---	1995	2	27	0.162
---	---	---	---	---	---	1995	3	33	0.319
---	---	---	---	---	---	1995	4	42	0.671
---	---	---	---	---	---	1995	5	47	0.898
---	---	---	---	---	---	1995	6	56	1.540